

ABSTRACT

OBERNUEFEMANN, KELSEY PIPER. Assessing the Effects of Scale and Habitat Management on Residency and Movement Rates of Semipalmated Sandpipers at the Tom Yawkey Wildlife Center, South Carolina. (Under the direction of Jaime A. Collazo.)

I evaluated the influence of inter-wetland distance and the timing of drawdowns on local daily survival (residency) and movement probability of Semipalmated Sandpipers (*Calidris pusilla*) during the springs of 2006 and 2007 at the Tom Yawkey Wildlife Center (YWC), South Carolina. There is growing interest in determining the scale at which coastal wetlands are functionally connected and how management influences their use by migrant shorebirds. Parameters of interest were estimated using multi-state models and encounter histories obtained from resight and telemetry data. Data were collected in the spatial context of three clusters of multiple wetland units each separated by distances of 2.6 to 4.1 km and two hydrologic treatments--a slow and fast draw down. Mean length of stay was 2.99 d (95% CIs = 2.45 - 3.52) in 2006 and 4.57 d (95% CIs = 2.59 – 8.92) in 2007. Residency probability was influenced by a negative and significant interaction between estimated percent fat at capture and southerly wind speed. This meant that differences in departure rates by birds with varying body conditions were minimized. Sixty-five percent of all marked birds stayed within 2 km from their banding location. Movement probabilities were negatively related to inter-cluster distance and bird density. In the spatial context of YWC there was functional connectivity among the clusters that were ~2.5 km apart; movement was negligible between units at nearly twice that distance (4.1 km). Contrary to expectations, the average probability of surviving and not moving for birds in slow-managed units was higher than birds in fast-managed units ($\Phi_{2006}^{SS} = 0.488$, $\Phi_{2007}^{SS} = 0.654$). On average, birds marked in fast-

managed units moved out at high rates ($\hat{\psi}_{2006} = 0.399$, $\hat{\psi}_{2007} = 0.467$). Higher prey biomass and bird density in slow-managed units influenced observed residency and movement rates. My findings advocate for conservation strategies that identify functionally connected wetland units and suggested that habitat supplementation for shorebirds during peak migration can be met by carefully planned staggered, slow drawdowns. The effectiveness of fast drawdowns is vulnerable to differential prey base quality, presence of birds on previously exposed habitat, failure of water control structures to operate properly, and the possibility of mismatching peak migration and rapid drawdown implementation.

Assessing the Effects of Scale and Habitat Management on the
Residency and Movement Rates of Migratory Shorebirds
at the Tom Yawkey Wildlife Center, South Carolina

by
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DEDICATION

To my Mom and Dad, Kim and Steve Piper, for teaching me to reach to for my dreams;

And to my husband, Jeff Obernuefemann, for making my dreams come true.

BIOGRAPHY

Kelsey Obernuefemann grew up in northern California and Cape Cod, Massachusetts, spending everyday after school in the woods behind her house where she kindled her interest in wildlife. She received her undergraduate degree in Environmental, Population, Organismic Biology from the University of Colorado at Boulder in 2002. Upon graduation, she worked with white-tailed deer and black bear, along with an influential internship with the U.S. Fish and Wildlife Service where she surveyed waterfowl and shorebirds, banded pelicans and terns, and decided that birds were in her future. From there she traveled the world to twenty-five countries on six continents, worked as an environmental educator, and explored and lived throughout the inter-mountain west, before coming to the Fish and Wildlife Coop Unit at North Carolina State University.

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THESIS INTRODUCTION

The life history of shorebirds renders them uniquely vulnerable to habitat loss and alteration due to their proclivity to concentrate at a small number of stopover sites during their annual migration (Myers et al. 1987). At each stopover site, northbound shorebirds strive to accumulate sufficient fat reserves to continue migration and reach the breeding grounds in good pre-reproductive condition. Consequently, one of the goals of the U.S. Shorebird Conservation Plan is to ensure that at these stopover sites there is both an adequate *quantity* of accessible habitat and that habitat is of high *quality* for migrating birds under intense time and energy constraints (Brown et al. 2001).

Small calidrid shorebirds require water depths between 0 to 4 cm to forage and are capable of responding rapidly to newly available habitat (Baker 1979, Rundle and Fredrickson 1981, Weber and Haig 1996, Davis and Smith 1998, Collazo et al. 2002). However, their ability to locate and move to new habitat is limited by the scale at which they perceive wetland landscape. Functional connectivity is a component of landscape connectivity, and it is dependent upon the behavioral responses of an organism to elements of the landscape (Tischendorf and Fahrig 2000). Researchers have recognized functional connectivity as a fundamental factor influencing the movement rate of shorebirds; such that a highly connected landscape enables more movement among habitat patches, and hence allows shorebirds to spend less energy searching for higher quality patches of food (Skagen 1997, Farmer and Parent 1997). High quality habitat can be made available through one of two water level drawdowns regimes during migration. A slow drawdown gradually lowers the water level in a managed unit to continuously provide newly accessible habitat

throughout the season, whereas a fast drawdown is implemented to augment accessible habitat quickly and is typically timed to match peak migration.

There have been no prior studies on how coastal shorebirds might perceive wetland connectivity at their spring stopover sites along the Atlantic coast. Likewise, while previous studies have examined the numeric response of shorebirds to different drawdown rates, none has quantified the functional (behavioral) response after the numeric response. Specifically, residency and movement probabilities reflect decisions made by shorebirds to take advantage of conditions that may facilitate maximizing prey intake. Such data would be useful to formulate management schemes at appropriate scales to ensure the availability of suitable habitat for spring migrants (see Skagen 1997), especially given that the Atlantic coast provides stopover habitat for an estimated 2.5 million shorebirds dependent on inland wetlands (Brown et al. 2001).

The goals of my study were to understand the influence of scale and habitat management at a spring stopover site on the movement (Ψ) and residency (S) rates of Semipalmated Sandpipers at the Tom Yawkey Wildlife Center, South Carolina. I conducted management experiments in 2006 and 2007 and used multistate models to estimate parameters of interest using encounter histories based on resight and telemetry data. I addressed three objectives: 1) determine the refuge-level residency rates of Semipalmated Sandpipers during spring migration, 2) determine the residency and movement rate of Semipalmated Sandpipers among three, spatially segregated wetland clusters, and 3) determine the residency and movement rate of Semipalmated Sandpipers between wetland units under two hydrologic treatments. Knowledge and insights gained from this work will

be useful to assess management tradeoffs, options and their conservation value to migratory shorebirds.

CHAPTER 1

Introduction

The demography of migratory shorebirds is uniquely vulnerable to habitat availability and quality due to their proclivity to concentrate at a small number of sites during their annual migration (Myers et al. 1987). During spring migration, coastal shorebirds utilize long “skips” or “jumps”, characterized by intensive fattening and abrupt departures at a threshold date from sites where food is abundant (Myers et al. 1987, Piersma 1987, Harrington et al. 1991). During this punctuated migration process, shorebirds have to decide whether to stay in the current wetland unit, move to a different unit, or leave the stopover site entirely and continue migration. Mean length of stay at these stopover sites may vary according to the birds’ arrival date (Warnock and Bishop 1998), body condition (Dunn et al. 1988), wind direction (Butler et al. 1997), and site quality (Schneider and Harrington 1981, Ydenberg et al. 2002). Site quality can be affected by prey availability (Farmer and Wiens 1999, Hicklin and Smith 1984), size of available habitat (Ydenberg et al. 2002, Pomeroy 2006) and amount of accessible habitat (Collazo et al. 2002). Studies also suggest that shorebird habitat use and migration strategies are influenced by the spatial context of wetlands and connectivity among them (Farmer and Parent 1997, Skagen 1997, Niemuth et al. 2006, Taft and Haig 2006a, b).

Landscape connectivity is the “degree to which the landscape facilitates or impedes movement among resource patches” and arises from complex interactions between landscape structure and organism movement behavior within a hierarchy of spatial scales (Taylor 1993, Goodwin 2003, Belisle 2005). Landscape connectivity is a function of both structural connectivity, which is independent of any attribute of the organism of interest, and functional

connectivity, which is dependent upon the behavioral responses of an organism to various elements in the landscape (Tischendorf and Fahrig 2000). Distance is an obvious example of an attribute independent of the organism. Conversely, the ability of the organism to overcome a barrier (e.g., flying over forested rather than open tracts) or initiate movement in response to the presence of other organisms, are examples of behavioral responses to elements in the landscape. Of course, there are limits to both forms of connectivity and these define the dispersers' performance (Doak et al. 1992, With et al. 1997, Tischendorf and Fahrig 2000). One must therefore determine the scale at which species respond to such elements, emphasizing that connectivity is species- and landscape-specific (Tischendorf and Fahrig 2000, D'Eon et al. 2002, Sanzenbacher and Haig 2002a, Belisle 2005).

A landscape's connectivity can determine foraging success when organisms, such as migrating shorebirds, forage over multiple patches (Goodwin 2003). Shorebirds can rapidly respond by arriving in newly exposed habitat in as little as 4 to 24 hours (Rundle and Fredrickson 1981, Collazo et al. 2002). Movement among patches can be costly due to the energy expended in searching for high quality sites; therefore a highly connected landscape reduces those costs and allows shorebirds to take advantage of more food patches (Farmer and Parent 1997, Belisle 2005). Valuable insights and advances in this area of research have been gained from studies of wintering (Sanzenbacher and Haig 2002a, b; Taft and Haig 2006a, b), breeding (Plissner et al. 2000, Haig et al. 2002), and mid-continental migrating shorebirds (Skagen and Knopf 1994a, b; Skagen 1997; Farmer and Parent 1997). For example, Farmer and Parent (1997) postulated that for Pectoral Sandpipers (*Calidris melanotos*), wetlands that were separated by >1100 m were functionally isolated. Movement rates between functionally isolated wetlands were ≤ 0.08 . Taft and Haig (2006a) suggested

that the influence of prey density on the distribution of wintering Dunlin (*Calidris alpina*) was most appropriately assessed on wetlands that were within 2 km of each other. Within this spatial scale, Dunlins concentrated in the most productive sites that were closer to a wetland neighbor. During a wet year the landscape context was unimportant because prey density was fairly uniform across wetlands.

There are no complementary data to make inferences about how coastal shorebirds in southeastern United States might perceive wetland connectivity at their spring stopover sites. Such data would be useful to formulate management schemes at appropriate scales to ensure the availability of suitable habitat for spring migrants (see Skagen 1997). The need for such data is further underscored by the fact that the Atlantic coast provides stopover habitat for an estimated 2.5 million shorebirds dependent on inland wetlands (Brown et al. 2001). However, additional work is needed to determine whether inferences from other studies can be generalized. Wintering and breeding birds may behave differently because they are under different time and energy constraints. Likewise, mid-continental spring migrants utilize different migration strategies due to the ephemeral nature of interior wetlands (Skagen and Knopf 1993, Skagen 1997).

In spring of 2006 and 2007, I evaluated the influence of scale and wetland management on shorebird residency and movement rates of Semipalmated Sandpipers (*Calidris pusilla*) at the Tom Yawkey Wildlife Center (YWC), South Carolina. These parameters express results in terms of structural elements of the landscape and the functional (behavioral) responses by shorebirds to the suite of factors considered in this study (Goodwin 2003). I used encounter histories of marked individuals and multi-state models to obtain parameter estimates (Kendall and Nichols 2004). At the broadest scale of analysis, the

refuge level (YWC), I modeled how body condition and patterns of southerly wind speed influenced residency rates. Residency rates or daily survival probability (\hat{S}) were defined as the probability that a bird, banded at the YWC on day i , remains to day $i+1$. I used percent body fat at capture to index body condition (Dunn et al. 1988). My interest in these factors stemmed from their importance in determining the number and duration of stops for migrant shorebirds and because wetland management is designed to improve the ability of migrants to meet their energetic requirements (Loech et al. 1995, Lyons and Haig 1995, Butler et al. 1997, Farmer and Wiens 1999, Åkesson and Hedenström 2000, Hostetler 2004, Lyons and Collazo in press).

At a smaller scale, or within refuge, I estimated residency and movement rates among clusters of wetlands (i.e., inter-cluster models). Residency rates (\hat{S}) were defined as the probability that a bird, banded at cluster j on day i , remains at YWC to day $i+1$. Movement rates (Ψ , $\hat{\psi}$) were defined as the probability that a bird, banded in cluster j on day i , moves to another cluster on day $i+1$. At this level I was interested in determining whether wetland clusters were functionally connected and the relative importance of site quality, distance, bird abundance, and size of wetlands in this process. Opportunities to assess the influence of scale were possible at YWC because its wetland units are arranged in three, spatially segregated clusters of multiple units each. While YWC did not contain replicate wetland contexts and inter-wetland distances as in studies by Farmer and Parent (1997) and Taft and Haig (2002a, b), it provided a landscape where some findings and predictions about connectivity could be explored further. For example, I tested whether wetland clusters at YWC were functionally connected given that the closest pair of clusters was separated by 2.6

km and the farthest by 4.1 km. Farmer and Parent (1997) suggested that wetland units were effectively isolated if movement rates among them was ≤ 0.08 . I also modeled the influence of bird density. Taft and Haig (2002a, b) quantified the relationship between bird density and prey density, and hinted at the possible role of bird density in attracting more birds to a wetland. A positive relationship might provide further evidence of how behavioral responses contribute to functional connectivity (Belisle 2005). I explicitly tested this possibility as shorebirds might be drawn to each other because they rely upon group foraging to facilitate prey detection and predator avoidance (Creswell 1994, Barbosa 1995, Lima 1995). Finally, I also estimated prey biomass (mg/cm^3) and accessible habitat (0-4 cm water depth) at each cluster. Estimates reflected the combined effects of two hydrologic manipulations: a slow or a fast drawdown. A slow drawdown gradually lowers the water level in a managed unit to make habitat accessible to foraging shorebirds throughout the season. A fast drawdown is implemented to augment accessible habitat quickly, typically timed to match peak migration. The individual influence of each hydrologic manipulation on shorebird residency and movement rates was addressed in Chapter 2.

Study Area

The Tom Yawkey Wildlife Center (YWC) is located in the Santee Delta-Cape Romain area of Georgetown County, South Carolina. It is a site of regional importance in the Western Hemisphere Shorebird Reserve Network. It harbors 5% of the flyway population or 20,000 individuals during the migratory season, including the Semipalmated Sandpiper (Marsh and Wilkinson 1991, Weber and Haig 1996). YWC is composed of approximately 8,000 hectares of marsh, maritime forest, upland pine forest, and ocean beach.

YWC's three main islands (North Island, South Island and portions of Cat Island) are separated from the mainland by the Intracoastal Waterway.

The study area was located on South Island (79°15'W, 33°10'N) and consisted of 13 brackish managed wetlands ranging in size from 12 to 69 ha. Each wetland unit has one primary, and in some cases, multiple secondary water control structures which allow managers to control the depth and drawdown rate of the wetland unit. Managed wetland units were characterized by gradually sloping bottoms of soft mud, surrounded by a perimeter ditch. While the majority of each wetland unit was open water, most have areas of widgeongrass (*Ruppia maritima*), sea purslane (*Sesuvium maritimum*), muskgrass (*Chara* spp.), saltmarsh bulrush (*Scirpus robustus*), black needle rush (*Juncus roemerianus*), smooth cordgrass (*Spartina alterniflora*), and giant cordgrass (*Spartina cynosuroides*) within the managed wetland unit (Weber and Haig 1996).

Managed wetlands were arranged in three sets of spatially segregated groups of wetland units, hereafter referred to as clusters (Figure 1). Cluster 1 consisted of three units, namely, Cooperfield (13 ha), Blackout Pond (34 ha) and Penfold Pond (22 ha). Cluster 2 consisted of the Southeast Goose Pasture (28 ha) and Southwest Goose Pasture (55 ha). Cluster 3 consisted of Upper Pine Ridge Pond (28 ha), Lady's Pond (12 ha), Santee Pond (45 ha), Twin Sisters Pond (65 ha), Lower Lower Reserve (18 ha), Middle Lower Reserve (69 ha), Upper Lower Reserve (27 ha) and Northern Reserve (23 ha) (see Table 1). During this study, clusters were treated alike in the sense that every cluster contained at least a pair of units under a slow and fast drawdown schedule or hydrologic treatment (see Chapter 2, Table 1). Within each cluster, units under study comprised the dominant or co-dominant feature in terms of suitable habitat for shorebirds. In clusters 1, 2, and 3, the proportion of wetlands

managed for shorebirds was 69%, 54%, and 45%, respectively. The remaining wetlands in the clusters were unsuitable for shorebirds they were either flooded or completely drawn down and hardened.

Methods

Bathymetric Profiles

Bathymetry maps were constructed for each wetland unit in 2006 because changes in vegetation cover had occurred since 1999 (date of the most recent available aerial imagery) and no prior bathymetric profiles of the wetland units had been created. Bathymetry data were used to estimate accessible habitat (0-4 cm water depth) for shorebirds as a function of gauge readings every week in 2006, and daily in 2007, during the migratory season. I initiated the process by recording depth and a GPS reading every 9-10 m along 2-4 transects that bisected each management unit (as in Figure 2). Transects were positioned to account for as much heterogeneity in each unit as possible. Each unit was subsequently photographed from the air (~700 m) using an unmanned aerial vehicle (UAV). The UAV was operated by a team from the University of Florida Cooperative Research Unit. Aerial photographs were then digitized and geo-referenced to digital ortho quater quads (DOQQs) of Yawkey Wildlife Center from 1999. Bathymetry data were then combined with the geo-referenced photos to produce maps depicting accessible habitat as a function of gauge readings.

Invertebrate Sampling

I sampled invertebrates three times in 2007 to obtain estimates of prey biomass for each wetland unit within each cluster. The initial sampling was conducted 17-18 May, closely matching peak of migration and implementation of the fast drawdown. Subsequent sampling events were a week apart (24-25 May; 31 May – 1 June). Invertebrates were collected from primary sampling plots, one in each wetland unit. Plots were aligned with the bottom contour of the managed unit to insure that “newly available habitat” would be sampled throughout the season. Each primary plot was 50 m x 5 m, subdivided into five secondary plots which were 10 m x 5 m. Within each secondary plot there were 50 subplots of 1 m². Within each primary plot, two 1 m² subplot sampling units were selected randomly during each sampling period and sampling was done “without replacement” because the subplots were altered during sampling (e.g., core sampling). A five-gallon bucket (radius = 13 cm, height = 36 cm) with the bottom cut out was used to isolate the water column, preventing the escape of any aquatic invertebrates. The bucket was pushed through the water and into the bottom substrate in a random location within the randomly chosen subplot. I pumped the water into gallon zip lock bags for transport back to the field house. Once the water was extracted from within the bucket, I used a hand bulb planter (radius = 3.75 cm, height = 10 cm) to extract two mud core samples from within the area contained by the bucket. Each core sample of mud was 5 cm deep. The benthic core samples were placed in zip lock bags for transport to the field house. At the field house, 20 cm diameter sieves down to 425 microns (W.S. Tyler Company, Mentor, OH) were used to separate the invertebrates from the water or mud substrate. The water and benthic invertebrates were kept separate and

placed in vials according the sample location and period, and preserved in a 10% formalin solution.

After the field season, the invertebrates were identified to either Class (Gastropoda, Polychaeta, Oligochaeta), Order (Amphipoda, Coleoptera, Diptera, Odonata, Trichoptera) or Family (Chironomidae, Corixidae) using a 20x dissecting microscope at North Carolina State University. Invertebrates were placed individually or in groupings of five on Millipore glass fiber prefilters, and then placed in a Precision Gravity Convection Oven for four hours at 70° C in order to remove any water. Dried invertebrates were weighed using a Thermo Electronic Microbalance to the nearest 0.1 mg. Dried weights for the invertebrates were expressed as a density in milligrams per cubic centimeters of either water or mud for each sample.

Mark-Encounter Histories

In 2006, 500 birds were captured with mist-nets and individually color-marked during 10 banding sessions (1-3 days each) from 10 May to 28 May. In 2007, 502 birds were captured and marked over 16 banding sessions conducted every other day from 7 to 18 May and every day from 18 to 28 May. Captured birds were kept in a ventilated cardboard box up to 2 hours or until all birds were processed. Birds were weighed to the nearest 0.5 g using a Pesola spring scale and measurements of their flattened wing chord (carpal joint to the wing tip to the nearest 1.0 mm) and bill length (bill tip to feather margin on forehead to nearest 0.5 mm) were also recorded. Colored bands were placed on the tibiotarsus. Birds were also outfitted with a metal USFWS band on their lower left leg (tarsometatarsus). This work was

conducted under IACUC (Institutional Animal Care and Use Committee) permit number: 06-039-O.

In 2006, data consisted only of encounters of color-marked shorebirds. Encounter history data were generated by recording unique color combinations of 4 Darvic UV resistant UPVC colored leg bands assigned to each captured bird (2 on right leg, 2 on left leg). In 2007, I supplemented color-marking with radio telemetry to increase the probability of detection, and thus, increase the likelihood of relating factors of interest in this study to shorebird responses. Low vegetation obstructed leg bands in some cases and some birds might have been missed if they occurred in the interior sections of the larger wetland units. Accordingly, 72 of the 502 Semipalmated Sandpipers captured in 2007 were also instrumented with transmitters. The 0.56 g radio transmitters (Model BD-2N Holohil Systems Ltd., Woodlawn, Ontario, Canada) were glued to the lower backs of each bird following methods described in Warnock and Warnock (1993). The radio transmitter was glued with waterproof epoxy (Liquid Bonding Cement, Torbot Group, Inc., Cranston, Rhode Island) to clipped feathers on the lower back about 5 mm anterior to the uropygial gland. The transmitters were less than the suggested 3% of a bird's body mass, and the retention time was expected be less than 7 weeks (Bishop et al. 2004). Transmitters were allocated among the 3 clusters of impoundments on a rotating 3 day schedule banding every day from 18 May to 28 May and split near evenly between slow (37 birds total) and fast treatments (35 birds total). I placed transmitters on 18 birds (slow $n = 11$, fast $n = 7$) in cluster 1, on 10 birds (slow $n = 5$, fast $n = 5$) in cluster 2, and on 44 birds (slow $n = 21$, fast $n = 23$) in cluster 3. Transmitters were allocated among clusters based on their relative acreage and Semipalmated Sandpiper population size (e.g., cluster 3 had the largest area and thus the

largest population of Semipalmated Sandpipers, while cluster 1 had the smallest area but the second largest observed population of Semipalmated Sandpipers).

Visual encounters (resights) in 2006 were obtained by surveying the study area every day (including banding day), except on three occasions when it was done at two day intervals to allow time for invertebrate sampling and shorebird surveys. Similarly, surveys in 2007 were performed every day (including banding days) except during invertebrate sampling days. Tracking of instrumented birds was done every day of the season. During resight surveys, all managed wetland units under treatment (approximately 425 ha) were searched from the dyke surrounding each unit, as well as by walking into the managed wetland units where substrate and water depths allowed. Telemetry searches were performed using R-1000 telemetry receivers (Communication Specialists, Inc., Orange, CA) with an RA-14K “H” style handheld antenna (Telonics, Inc., Mesa, AZ). Tracking was done in teams of two to simultaneously locate telemetered birds using triangulation from 14 pre-determined listening stations placed throughout the study area.

Bird Population Index

Weekly shorebird counts were conducted to obtain an idea of changing population numbers at YWC. However, because I could not sample each of the wetland units in their entirety, I made counts from three randomly located survey points at each managed wetland unit and treated it as an index of the population density. Counts at each managed wetland unit were made within a 100 m radius fixed area of the point to standardize results (birds/unit area). Within the 100 m area, I assumed that detection was 1 or nearly so.

Wind

The possible influence of “southerly winds” on shorebird residency was modeled using an expression that excluded all winds that could be considered “head winds” or those less than 90 degrees or greater than 270 degrees. Winds from a southerly direction might aid northbound shorebirds in their movement among stopover areas (Butler et al. 1997). This covariate was calculated as $swind = -\sum v_i \cos\theta_i I_i$, where $I_i = 1$ if $\cos\theta_i$ is < 0 , otherwise $I_i = 0$ (J. E. Lyons, Patuxent Wildl. Res. Ctr, pers. comm.). The closest source of wind data to YWC was the Charleston International Airport, 80 km south of YWC. Hourly surface wind data were collected by the National Climatic Data Center. Surface winds were used because they are the cues birds on the ground use to identify winds aloft (Skagen and Knopf 1994b, Åkesson and Hedenström 2000, Liechti 2006).

Data Analysis

Shorebird count data (birds/ha) were analyzed using ANOVA with survey, cluster, and the interaction survey*cluster as model terms (JMP 1994). The response variable was log transformed to meet homogeneity of variances assumption. Similarly, invertebrate data were analyzed using ANOVA with the response variables being the biomass of invertebrates (all taxa) in the water column, muddy substrate, or combined (all taxa, all substrates). Model terms were sampling period, cluster, wetland unit within cluster and sampling period * cluster interaction (JMP 1994). Data were power-transformed ($^0.95$) to meet homogeneity of variances assumption.

I combined invertebrate taxa by substrate because 60% of all taxa were represented (shared) among clusters and because prey biomass for most taxa did not differ among

clusters or substrate (Appendix I). Semipalmated Sandpipers are known to prey on all of the prey items found in YWC (Weber and Haig 1996), and like most migratory shorebirds, they are known for their dietary flexibility (Skagen and Oman 1996, Parrish 2000). Therefore, it is unlikely that pooling data by substrate masked the influence of any particular prey item on foraging patterns by migrant Semipalmated Sandpipers in response to drawdown schedules. This possibility was further minimized because every cluster contained multiple units under various levels of accessible habitat and because treatments to most managed units were re-assigned between 2006 and 2007.

The weight and wing chord measurements were used to calculate estimated percent fat (epf), which is a body condition index for each bird based on the equation $epf = 100 \left(\frac{WT - FFW}{WT} \right)$, where WT is the total body weight and FFW is the fat-free weight (Page and Middleton 1972, Dunn et al. 1988). Fat-free weights were calculated based on the equation $FFW = -9.0513 + 0.3134 (\text{wing length})$ (Page and Middleton 1972). The estimated percent fat (epf) dataset, then, was divided into nine sampling occasions each year (May 7-10, May 16-17, May 18, May 19, May 20, May 21, May 24-25, May 26, and May 27-28). I examined patterns of variation between years and sampling occasion using ANOVA with year, sampling occasion, and the interaction year*occasion as model terms with epf as the response variable (JMP 1994). Inter-cluster variation in epf in 2007 was examined with ANOVA. Cluster and sampling occasions (and interactions) were the main effects (JMP 1994).

Residency Rates – Refuge Level Assessment

In 2006, I estimated residency rates based on encounter histories from visual recaptures or resight data. I combined encounter histories from resight and telemetry data in 2007. A joint analysis of the two data types, referred to as group (*g*) in models, has the advantage of increased precision of estimates as well as the ability to test for differences in the encounter rates of the two cohorts (Nasution et al. 2001). I used the “recaptures only” module in Program MARK (White and Burnham 1999). In 2006, there were 22 sampling occasions, or 21 intervals. In 2007, there were 24 sampling occasions or 23 intervals. Every sampling occasion represents a complete search of the refuge. In most cases this search took 1 day, but in a few instances complete coverage took 2 days. I also estimated the mean length of stay (MLS) of shorebirds each year using: $MLS = -1/\ln(\text{daily residency probability})$ (Brownie et al. 1985). Estimates should be taken only as an approximation of MLS because this formula assumes constant survival and previous work modeling shorebird residency rates has shown that rates vary seasonally (Dinsmore and Collazo 2003, Lyons and Collazo 2005). Estimates reported herein are based on the seasonal average of daily residency probabilities.

I examined 12 models of residency and recapture rates for 2006. These include reduced parameter models and “pre-defined” (i.e., naïve) models that included constant and time-specific residency and constant recapture rates. Naïve models $[S(t), p(t)]$ and $[S(.), p(t)]$ were not included on the final list due to the high number of intervals for which the parameter was non-estimable. Two covariates were used to model residency rates—estimated percent fat (epf) and southerly wind speed (Swind). While epf was measured only at capture, 500 birds were captured throughout the season. Thus, I also explored the possible interaction between epf and Swind.

Finally, I also explored whether residency rates were best described by a linear (T) or curvilinear (TT) trend (sensu Dinsmore and Collazo 2003, Lyons and Collazo 2005). I used the median \hat{c} procedure in MARK to estimate the variance inflation factor. I used the Akaike's Information Criterion modified to account for small sample size to select the most parsimonious model (Burnham and Anderson 2002). Models with $QAICc \leq 2$ were considered models with highest support. The *a priori* model set evaluated for 2006 is listed below.

S {(.)}, p {(.)}
S {(t)}, p {(.)}
S {(T)}, {p (.)}
S {(TT)}, {p (.)}
S {(epf)}, {p (.)}
S {(Swind)}, {p (.)}
S {(TT+epf)}, p {(.)}
S {(TT+epf+TT*epf)}, p {(.)}
S {(TT+Swind)}, {p (.)}
S {(TT+epf+Swind)}, {p (.)}
S {(epf+Swind+Swind*epf)}, {p (.)}
S {(TT+epf+Swind+Swind*epf)}, {p (.)}

Similarly, I examined 20 models of residency and recapture rates for 2007. These models differ from 2006 in that encounter histories were made up visual (i.e., resight) and telemetry data. Recapture rates were modeled either by encounter source (i.e., group) or disregarding source (i.e., combined). I did not include $\{(g*t)\}$ models on the list due to the high number of non-estimable parameter intervals. Naïve models accounting for detection probability by source (i.e., $\{p(g)\}$) ranked higher ($QAICc$) than constant $\{p(.)\}$ or time-varying models $\{p(t)\}$. Therefore, survival was modeled with recapture probabilities by source. The *a priori* model set evaluated for 2007 is listed below.

$S \{(.)\}, p \{(.)\}$
 $S \{(.)\}, p \{(t)\}$
 $S \{(t)\}, p \{(.)\}$
 $S \{(t)\}, p \{(t)\}$
 $S \{(g)\}, p \{(.)\}$
 $S \{(g)\}, p \{(t)\}$
 $S \{(.)\}, p \{(g)\}$
 $S \{(g)\}, p \{(g)\}$
 $S \{(t)\}, p \{(g)\}$
 $S \{(epf)\}, p \{(g)\}$
 $S \{(Swind)\}, p \{(g)\}$
 $S \{(T)\}, p \{(g)\}$
 $S \{(TT)\}, p \{(g)\}$
 $S \{T+epf+T*epf\}, p \{(g)\}$
 $S \{TT+epf+TT*epf\}, p \{(g)\}$
 $S \{(T+epf)\}, p \{g\}$
 $S \{(T+Swind)\}, p \{g\}$
 $S \{(T+epf+Swind)\}, p \{g\}$
 $S \{(T+epf+Swind+Swind*epf)\}, p \{g\}$
 $S \{(epf+Swind+Swind*epf)\}, p \{g\}$

Inter-Cluster Residency and Movement Rates

Residency and movement rates were estimated using encounter histories generated in 2007 by both resight (collected from 8 May to 11 June) and telemetry (collected from 18 May to 11 June) techniques. Encounter histories were coded by cluster. Treatment within cluster was ignored because each cluster was treated alike in that each contained wetlands under both slow and fast drawdowns. I expressed accessible habitat (ha) in relative terms (i.e., proportion in cluster of interest/sum of accessible habitat in all clusters) to account for the fact that each cluster had a different areal extent. Inter-cluster distance was the nearest neighbor distance from the perimeter of each cluster to the closest point of a neighboring cluster's perimeter measured using ArcGIS software (Farmer and Parent 1997). The distance between clusters 1 and 2 was 4.1 km; between clusters 1 and 3 was 2.8 km; and between clusters 3 and 2 was 2.6 km.

Seven covariates were used to model residency and movement rates. These were estimated percent fat (epf), southerly wind speed (Swind), prey biomass (mg/cm^3), index of bird density (birds/ha), proportion of accessible habitat in cluster of interest/sum of accessible habitat in all clusters, total area in each cluster (ha), and average distance between each set of two clusters (m). Estimated percent fat and southerly wind speeds were used only to model its influence on residency rates. Conversely, total area of individual clusters (ha) and average distance between sets of clusters were used only to model their influence on movement rates. These covariates were modeled as additive effects on either constant or time-varying S and Psi models using reduced parameter models. Time-varying models also included linear (T) or quadratic (TT) terms as it has been shown the residency rates may vary in a curvilinear fashion (e.g., Dinsmore and Collazo 2003) and I hypothesized that movement rates might increase or decrease as a function of MLS. Wind and accessible habitat data were collected on every sampling occasion and manually entered to model their effects on time-varying S and Psi using reduced parameter models. Bird density index and prey biomass data were collected on fewer occasions due to field logistic constraints. Bird density index was estimated weekly on five occasions; prey biomass was estimated on three occasions. Although I acknowledge that this was a limitation, my goal was primarily to gain insights about the influence of these variables on a time varying context with as many estimates as logistics permitted. To minimize spurious interpretation of results, data were collected in the shortest possible intervals and were closely aligned with migration events and treatment implementation. For example, prey was first sampled on 17-18 May 2007, closely matching peak shorebird migration and implementation of the fast drawdown. Subsequent sampling events were on 24-25 May and 31 May – 1 June, a week apart. I also constructed two sets of models that reflect the interaction between body

condition (epf) and southerly wind speeds (Swind), and prey biomass and accessible habitat (site quality interaction). The rationale for the interaction between epf and wind covariates was outlined above. The rationale for the interaction between prey and access stems from the fact that prey for Semipalmated Sandpipers occurs in both the water column and muddy substrate. As such, patterns of prey richness and density may vary with water levels. It follows that foraging quality might be highest when physical conditions allow shorebirds to forage in both substrates simultaneously (e.g., $\leq 0\text{-}4$ cm water depth).

I constructed 54 models to evaluate variation in residency rates (\hat{S}) and movement rates (Φ , $\hat{\psi}$). The *a priori* model set included pre-defined (i.e., naïve) models as well as reduced parameter models (Appendix II). Naïve models $\{S(t), p(g^*t), \Psi(t)\}$ and $\{S(g^*t), p(g^*t), \Psi(g^*t)\}$ were not included because the number of non-estimable intervals was high. Analysis was done using the “multi-strata recaptures only” module in Program MARK (White and Burnham 1999). I used the Akaike’s Information Criterion to select the most parsimonious model (Burnham and Anderson 2002). Models with $\Delta\text{AICc} \leq 2$ were considered models with highest support. I could not obtain an estimate \hat{c} to adjust models for overdispersion, much of it probably stemming from the gregarious behavior of shorebirds. Some models had observed \hat{c} values of 4.28 to 5.20. Values ≥ 3 suggest that there is a possibility that some models might not receive higher support when in fact they should (Lebreton et al. 1992). As suggested by Cooch and White (2006), I assessed the sensitivity of top models to incremental values of median \hat{c} (e.g., 1.5, 2.0, 2.5). This ad hoc process leads to more conservative model selection (i.e., fewer parameters) and can suggest if other models should have received greater support. Adjustments re-ordered the top

2 models ($\Delta\text{AICc} \leq 2$). However, models were exactly alike except that for one parameter (T vs. TT term). Since the number of models explored was large, I only report those with a $\Delta\text{AICc} \leq 10$ (Burnham and Anderson 2002). Finally, I used estimates of S and Psi to separate movement and residency probabilities by cluster (Cooch and White 2006). I was interested in depicting the probability of a shorebird surviving and not moving from a particular cluster (i.e., $\hat{\Phi}^{11}$, $\hat{\Phi}^{22}$ or $\hat{\Phi}^{33}$). Expressing results in this fashion should aid readers to discern better the relationship between site quality, distance and management.

Careful consideration of four model assumptions is important to interpreting these results. First, I assumed that every color-marked bird had the same probability of being resighted in sampling period i and that every marked bird had the same probability of surviving from sampling period i to $i+1$, assuming that it was alive and present in the population at the time the survey was conducted. The same applied to instrumented birds. Second, I assumed that emigration (i.e., departure) was permanent. I believe that this assumption was met because coverage of the study areas was frequent and surveys included all available shorebird habitat at YWC, reducing chances that color bands or instrumented birds were overlooked (e.g., temporary emigration). Support for my assumption also comes from the work of Lyons and Collazo (2005). They found no evidence of temporary emigration problems during their study of telemetered Semipalmated Sandpiper at YWC in 2001 after routinely checking adjacent wetlands during aerial surveys. Some birds might have emigrated to near-by sandbars and mudflats adjacent to South Island in Winyah Bay and along the ocean beach (Weber and Haig 1996), but these areas are used for roosting. Foraging takes place primarily within YWC. Third, I assumed that marks (i.e., color bands, transmitters) were not lost and that in the case of color bands, all were correctly recorded.

This assumption was corroborated at least for transmitters—no losses were recorded during this study. Parameter estimates were reported as estimate \pm standard error.

Results

Total counts (birds/ha) of Semipalmated Sandpipers peaked around 15 May in 2006. Counts did not differ among clusters ($F = 0.762$, $df = 2, 57$, $p = 0.471$; Figure 3). Seasonally, counts in cluster 3 were fairly consistent in comparison to greater variability in the other two clusters (Figure 4). The average estimated percent fat (epf) in 2006 was 9.07 (SE = 0.58) whereas in 2007 it was 9.27 (SE = 0.51). As the season progressed, newly captured birds had higher epf values ($F = 21.45$, $df = 17, 760$; $p < 0.0001$). In 2007, epf was significantly greater in cluster 1 than in either of the other clusters ($F = 8.26$, $df = 2, 499$; $p < 0.0003$).

Southerly winds were recorded with greater frequency in 2006 (65%) than in 2007 (45%). In 2007, winds from the south averaged 14 km/h (SE = 0.21), increasing at a rate of 0.08 km/hr/day throughout the migratory season (SE = 0.02; $F = 5.49$, $df = 1, 19$, $p = 0.03$). Highest rates of departure (i.e., low residency) were associated with highest wind speeds (Figure 5). A notable exception was recorded in May 20th. Daily accessible habitat (ha) in each of the three clusters of wetland units increased seasonally as the water level was drawn down to accommodate migrating shorebirds (Figure 6). The marked decrease in accessible habitat on June 2 and 3 in 2007 was caused by a rainfall event of ~6.35 cm.

Prey biomass (mg/cm^3) increased gradually as the season progressed, but not significantly ($F = 0.369$, $df = 2, 33$, $p = 0.69$), see Appendix 1 for details). Prey biomass in the mud core was not significantly different among clusters ($F = 0.765$, $df = 17, 17$, $p =$

0.12). However, prey biomass in the water column was significantly higher in cluster 3 than either clusters 1 or 2 ($F = 2.491$, $df = 17, 18$, $p = 0.009$).

In 2006, residency rates were best described by a model with a curvilinear trend in residency rates (TT), estimated percent fat, southerly wind and an interaction between estimated percent fat and southerly wind (i.e., lowest QAICc weight = 0.47, Table 2). The variance inflation factor was $\hat{c} = 1.02$. Visual encounter probability was constant (0.082; 95% CIs = 0.063 - 0.105). The interaction between epf and southerly wind speed was significant and negative ($\hat{\beta} = -0.0177$; 95% CIs = -0.0329 - -0.0026; Table 3). The effect of the interaction between epf and the speed of southerly winds was to minimize the difference in residency rates between high and low epf values. This was illustrated by predicted values of daily survival probability as a function of the average high and low values of epf (Figure 8). Seasonal residency probabilities and MLS for 2006 are depicted in Figure 7. The seasonal MLS was 2.99 days (95% CIs = 2.45 - 3.52). Based on QAICc (≤ 2.0), a second plausible model featured the effects of epf and Swind (Table 2).

In 2007, residency rates were best described by a model that included a linear trend in residency rates (T), estimated percent fat, southerly winds, and the interaction between epf and southerly winds (QAICc weight = 0.54, Table 4). The variance inflation factor was $\hat{c} = 1.187$. Encounter probabilities varied by group (i.e., resight, telemetry). Estimates of encounter probability were 0.113 for resight (95% CIs: 0.091 – 0.138) and 0.702 (95% CIs: 0.643 – 0.754) for telemetry. The interaction between epf and Swind was significant but negatively related with daily survival ($\hat{\beta} = -0.0088$, 95% CIs = -0.0169 to -0.0008; Table 5). Seasonal residency probabilities and mean length of stay for 2007 were depicted in Figure 9.

The mean length was 4.57 days (95% CIs = 2.59 – 8.92). One other model could be considered a plausible alternative (i.e., QAICc \leq 2.0). It featured a linear trend in residency rates, epf and Swinds and recapture probabilities by group (Table 4).

Twenty-seven percent of all color marked and instrumented Semipalmated Sandpipers did not move from the site where they were captured. Cumulatively, 60% did not move more than 1 km, 65% no more than 2 km, and 83% did not move more than 4 km (Figure 10). No bird moved was observed to move farther than 6.5 km while at the YWC. The greatest distance a bird could possibly have moved among wetland units 7.9 km. The mean maximum distance that a bird moved from where it was captured was 1.63 km (95% CIs = 1.33 - 1.94).

Inter-cluster residency and movement rates were best described by a model that accounted for variation in residency rates by a quadratic term (TT), estimated percent fat, southerly wind speed, their interaction (epf*Swind), the proportion of accessible habitat, prey biomass, and their interaction (access*prey) (AICc weight = 0.46; Table 6). The interaction between epf and Swind was significant and negative ($\hat{\beta} = -0.0087$, 95% CI = -0.0172 to -0.0004; Table 7). The interaction between prey and access was not significant ($\hat{\beta} = -0.536$, 95% CIs = -1.079 – 0.006). Variation in movement probabilities was negatively related to the distance between clusters and the density of birds in any given cluster (Table 7). Encounter probabilities in this model were best described by group (i.e., resight or telemetry), cluster and size of cluster (Table 6). Recapture probabilities were 0.08 (resight) and 0.65 (telemetry) in cluster 1, 0.09 and 0.66 in cluster 2, and 0.11 and 0.72 in cluster 3. Based on Δ AICc (\leq 2.0), there was one alternative model. The second best model was

similar to the top model, except that it included a linear trend (T) in the residency probability (AICc weight = 0.33; Table 6).

Residency patterns of shorebirds were not significantly different, although rates in cluster 3 decreased noticeably after sampling occasion 5-6 (Figure 11). Seasonal mean length of stay for cluster 1 was 7.72 d (95% CIs = 5.27 - 10.17), for cluster 2 it was 6.13 d (95% CIs = 3.68 - 8.58), and for cluster 3 it was 3.87 d (95% CIs = 1.42 - 6.32). The probability of moving away from the cluster birds were captured was negatively and significantly related to the number of birds in clusters ($\hat{\beta} = -1.9002$, 95% CI = -2.6573 - -1.1431) and the distance among clusters ($\hat{\beta} = -1.5955$, 95% CI = -2.3871 - -0.8038). Rates of movement away from clusters 1 to 3 and 2 to 3 were positive and significant (Figure 12, Table 7). Movement away from cluster 1 to 3 decreased around 20 May, when a wetland unit (13 ha) became accessible. In contrast, the marked movement out of cluster 2 to 3 was associated with the gradual desiccation of larger portions of cluster 2. Patterns of the probability of surviving and not moving per cluster (e.g., Φ^{11}) reflected the aforementioned movement rates (Figure 13).

Discussion

Refuge- and cluster-level analyses of residency rates highlighted the significant and negative interaction between epf and Swind. This meant that the possibility of differential departure rates as a function of body condition was minimized. Put in another way, strong southerly winds effectively created an even playing field of residency for either 2006 or 2007, regardless of body condition. This interaction provided a plausible explanation to account for departures of Semipalmated Sandpipers from a stopover with greatly varying fat

loads (Skagen and Knopf 1994b). My findings were in concert with studies that have noted that birds will preferentially depart from a stopover site during tailwinds, thus minimizing the energetic cost of migration (Butler et al. 1997, Åkesson and Hedenström 2000). Findings were also in concert with predictions of the time-minimization hypothesis that purport that the motivation to stay or leave a stopover site has less to do with body condition and more to do with the biological clock within the bird to reach the breeding grounds at the “appropriate” time (Åkesson and Hedenström 2000).

Some remarks about the “main effects”, epf and Swind, are warranted. The positive relationship between epf and residency rates was counterintuitive because time minimization theory suggests that birds should depart from a stopover as soon as the “optimal” fuel load is attained (Alerstam and Lindström 1990). It follows that birds with higher epf at capture could depart sooner than those with lower values. However, due caution should be exercised when evaluating single factor hypotheses such as this one. First, the relationship between epf and residency rates might interact with extraneous factors such as wind speed and direction as my findings and those of others have suggested (see above). Second, a stopover might contain cohorts of birds with different migration strategies. Warnock and Bishop (1998) found interior migrating Western Sandpipers had a length of stay that was three times shorter and traveled significantly leaner than neighboring coastal cohorts of the same species. Third, epf does not provide information on the fat deposition rate of the bird. It is possible that a bird with a low epf at capture may have a higher fat deposition rate than birds with a higher epf and achieve departure fuel loads more quickly and depart sooner (Weber and Houston 1997). It is for this reason that researchers interested in establishing tighter relationships

between body condition and habitat quality are exploring other tools such as plasma metabolites (e.g., Guglielmo et al. 2005, Lyons and Collazo in press).

My analyses were predicated on the assumption that wind patterns at YWC were correlated with those recorded at the nearest source of wind data 80 km south of YWC. Under this assumption, the negative relationship between Swind and residency rates recorded in 2006 was consistent with “wind-assisted” departures from stopover areas (Weber et al. 1998; Åkesson and Hedenström 2000). The positive relationship in 2007 relationship was not. The positive relationship probably arose because southern winds slightly but consistently increased during the season. This wind pattern was matched by increasing seasonal residency rates, which decreased as season tapered off. Wind patterns in 2007 were noteworthy because the opportunities for “wind-assisted” departures were substantially fewer than in 2006. Weber et al. (1998) and Åkesson and Hedenström (2000) showed that departure rates were also influenced by the probability of encountering southern winds. The frequency of southerly winds in 2007 was 45% as compared to 65% in 2006. Frequency was not addressed by the Swind covariate; it only reflected average wind speed. The implications of these inter-annual differences are that some migrants with “optimal” fuel loads might depart the area at higher energetic costs because there are fewer wind-assisted opportunities (Weber et al. 1998, Åkesson and Hedenström 2000). This possibility was documented on 20 May 2007 when there were high departure rates and lowest recorded southerly wind speeds.

Model selection at the inter-cluster level underscored that residency rates can and should be influenced by prey biomass and amount of accessible habitat (and their interaction). Shorebird distribution is strongly influenced by the availability of food, especially during migration (Evans 1976, Kersten and Piersma 1987, Colwell and Landrum

1993, Placyk and Harrington 2004), and this process is mediated by the amount of accessible habitat. Small shorebirds, such as Semipalmated Sandpipers, require water depths between 0-4cm (Baker 1979, Weber and Haig 1996, Davis and Smith 1998, Collazo et al. 2002). Although the influence of prey biomass and accessible habitat on residency rates was not statistically significant, their potential importance is better appreciated when movement rates were assessed. The point was further underscored when survival and movement were decoupled and expressed as ϕ (Φ).

Shorebirds moved primarily from clusters 1 or 2 to cluster 3. Movement from cluster 3 to either cluster was negligible (average rate = 0.03, 95% CIs = 0.027 – 0.034). I documented at least three examples of variation of environmental conditions related to prey and access that contributed to these patterns. First, water-column prey biomass in cluster 3 was significantly greater than in clusters 1 and 2. Differential levels of prey biomass among clusters resulted from prey concentration as water was drawn down. This differential could have contributed to observed movements and residency patterns because shorebirds are attracted to areas of higher food availability and are less likely to seek out alternative habitat patches once there (Hicklin and Smith 1984, Colwell and Landrum 1993, Farmer and Parent 1997, Placyk and Harrington 2004, Taft and Haig 2006a). Second, a significant decrease in movement away from cluster 1 was related to an increase of accessible habitat induced by the implementation of a fast drawdown in the Cooperfield unit. The quick response of shorebirds to variations in accessible habitat was in concert with previous work on managed wetlands (e.g., Rundle and Fredrickson 1981, Collazo et al. 2002). Third, movements from cluster 2 were associated with persistent desiccation of its wetland units. While this pattern increased accessible habitat, the hard-pan and cracked mudflats were unsuitable for shorebird

foraging despite the numerous gastropods encased within the dried mud in Southwest Goose Pasture. In contrast to clusters 1 and 2, I suggest that the low probability of movement away from cluster 3 was due to the higher number of units within the 285 ha cluster. While prey and access varied among units within the cluster, the greater number of units likely dampened marked quality fluctuations.

Inter-cluster distance and bird density influenced movement among clusters significantly. As indicated above, site quality in clusters 1 and 2 changed seasonally and shorebirds moved to the closest unit, cluster 3, consistent with the negative and significant influence of distance featured in top models. These clusters were 2.6-2.8 km apart. Farmer and Parent (1997) suggested that functional connectivity began to weaken around 1.1 km, whereas Taft and Haig (2006b) suggested that it occurred at distances > 2 km. Although my findings suggested that structural connectivity was achieved at slightly longer distances, by and large, they were consistent with the aforementioned studies. In sharp contrast, when the distance was nearly twice as long (4.1 km) movement rates was negligible. Rates between cluster 1 and 2 averaged 0.045 (95% CIs = 0.032 – 0.058) and between cluster 2 and 1 they averaged 0.052 (95% CIs = 0.038 – 0.067). These rates were lower than those reported by Farmer and Parent (1997) for functionally isolated wetlands in the mid-continent (~ 0.08). The fact that movement rates between cluster 2 and 1 were low, particularly when accessible habitat was made temporarily available in cluster 1 (i.e., Cooperfield), provided compelling evidence that both clusters were effectively isolated from each other.

The negative influence of bird density over movement rates provided evidence of the importance of behavioral mechanisms in the context-dependent role of functional connectivity for Semipalmated Sandpipers (Belisle 2005). The mechanism by which this

influence might be exerted is related to the flocking behavior of Semipalmated Sandpipers. The phenomenon of flock formation is generally explained by two hypotheses. One purports that flocking increases foraging efficiency through the communal discovery of new food patches; and the second, that flocking enhances predator avoidance through shared vigilance and/or dilution effects (Barbosa 1995, Lima 1995). It is believed that the feeding vocalizations of these flocks attract more birds and convey an “all is well” signal that reduces individual vigilance and allow for more attention to feeding (Kushlan 1976, Battley et al. 2003). Shorebirds might balance the benefits of energy intake with the costs of predation by choosing habitats that will provide afford greater safety (Cresswell 1994, Barbosa 1995, Ydenberg et al. 2002, Pomeroy 2006). This benefit is more likely accrued in sites with greater shorebird numbers.

My findings advocate, as have others before (Skagen and Knopf 1994, Farmer and Parent 1997, Niemuth et al. 2006, Taft and Haig 2006b), for shorebird conservation strategies that identify functionally connected wetlands. These landscapes allow shorebirds to spend less energy searching for higher quality patches of food (Farmer and Parent 1997). Striving for functionally connected wetlands also advocates for coordinated management. Movement and residence options at YWC were likely enhanced because clusters of wetlands across the landscape were managed alike. Not only do multiple wetland complexes allow for more habitat heterogeneity, but they also can increase foraging success when organisms, such as migrating shorebirds, forage over multiple patches (Goodwin 2003). Multiple options of suitable habitat in a stopover such as YWC also augment the probability that birds will remain at the site for as long as necessary, minimizing risks associated with searches of alternative wetlands (Clark and Butler 2001, Hostetler 2004). Finally, integrated

management may also provide greater flexibility to refuges that have competing priorities. For example, a substantial number of wetland units might have to be managed for other objectives (e.g., controlling or promoting SAV). In such circumstances, connectedness with neighboring clusters of wetlands or refuges could minimize unnecessary departures from the shorebird conservation area of interest.

This study quantified how the spatial configuration of wetlands, bird density, and site quality influenced residency and movement rates of Semipalmated Sandpipers at a stopover of regional importance. In the process, it established that clusters of wetlands at YWC were functionally connected at a distance of ~2.5 km (*sensu* Goodwin 2003, Belisle 2005). Few studies have explicitly examined the scale at which small, coastal shorebirds perceive wetland connectivity (e.g., Butler et al. 2002, Taft and Haig 2006). My study contributed to this growing body of knowledge by measuring functional (behavioral) responses of shorebirds to structural elements of the landscape (Goodwin 2003, Belisle 2005). Functional connectivity in my study area broke down at 4.1 km. Because my work was not spatially replicated, I could not discern where, between 2.5 and 4.1 km, connectivity breaks down. Spatial replication and more frequent invertebrate sampling (\geq weekly) are elements of study design for future studies that could help strengthen our understanding of the functional connectivity among managed wetlands.

Table 1. List of managed wetland units at the Tom Yawkey Wildlife Center, South Carolina in 2006 and 2007. The size (ha) of managed wetland units, the cluster where it belonged, and an identification number are listed. The identification number corresponds to each unit's number in Figure 1.

Managed Wetland Unit	Unit Map Number	Size (ha)	Cluster
Cooperfield	1	13	1
Blackout Pond	2	34	1
Penfold Pond	3	22	1
Southeast Goose Pasture	4	28	2
Southwest Goose Pasture	5	55	2
Northern Reserve	6	23	3
Lady's Pond	7	12	3
Upper Lower Reserve	8	27	3
Middle Lower Reserve	9	69	3
Lower Lower Reserve	10	18	3
Twin Sisters Pond	11	65	3
Santee Pond	12	45	3
Upper Pine Ridge Pond	13	28	3

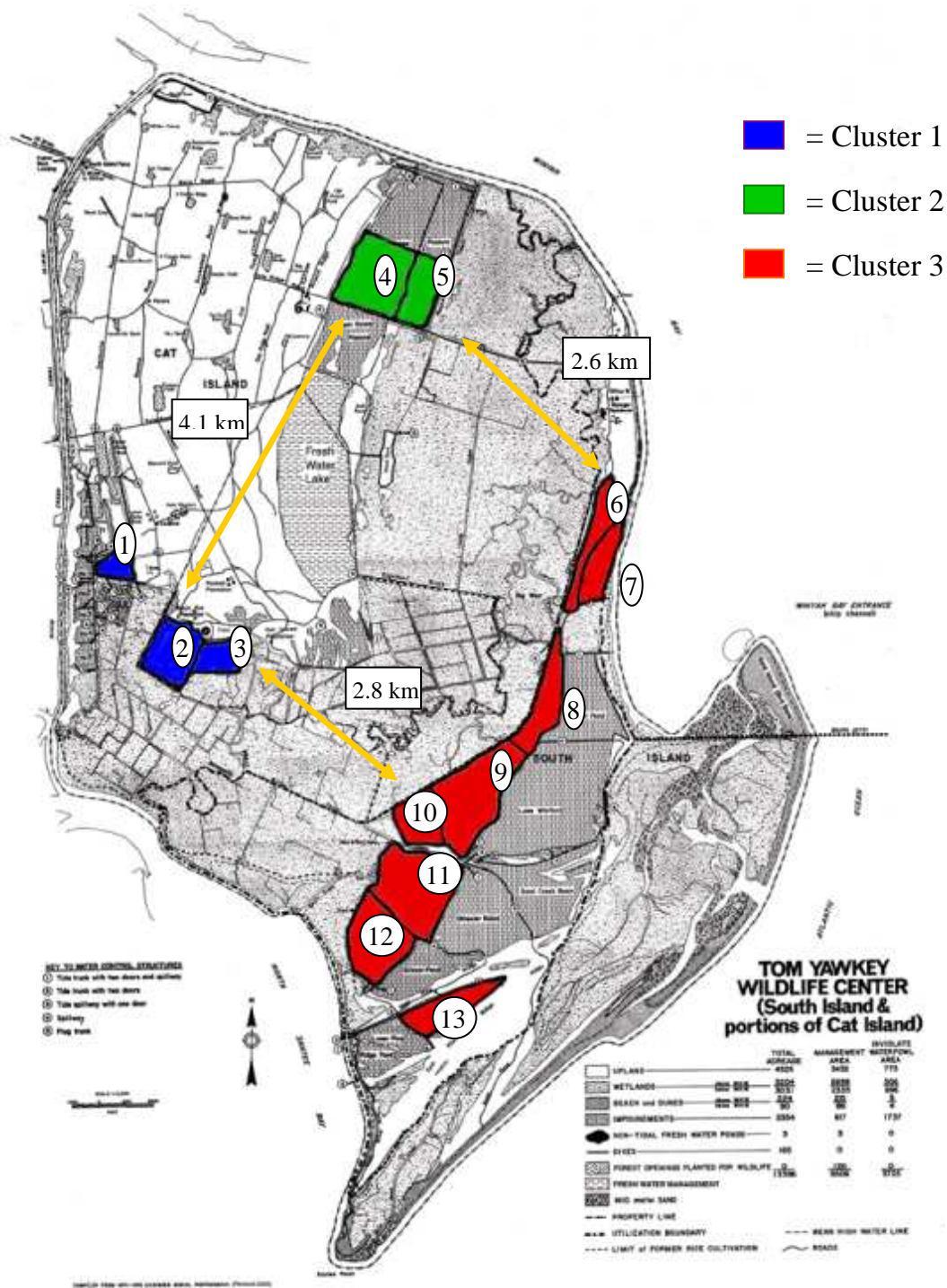


Figure 1. Map of the Tom Yawkey Wildlife Center, South Carolina showing the location of managed wetland units to estimate residency and movement rates of Semipalmated Sandpipers during Spring migration of 2006 and 2007. Clusters of managed wetland units are indicated by different colors, with inter-cluster distances displayed. Managed wetlands were numbered to correspond to Table 1.

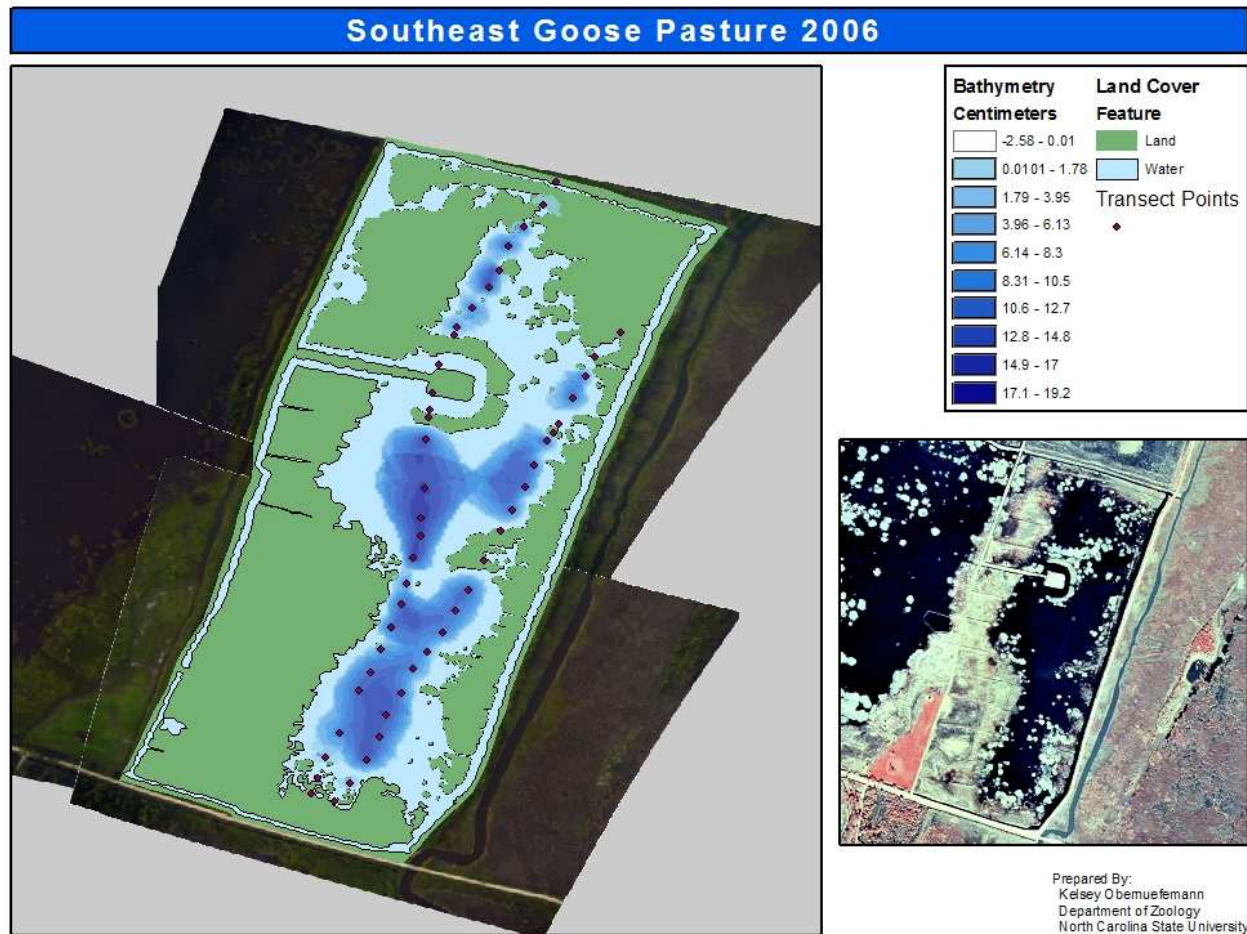


Figure 2. Bathymetry map of the Southeast Goose Pasture wetland unit at the Tom Yawkey Wildlife Center, South Carolina. The image on the left depicts the transects walked with GPSed depth reading locations (red) and the resulting bathymetric profile of the flooded areas and the extent of vegetation as per digitized 2006 aerial photographs. The image inset on the right is the 1999 satellite orthophoto. Visual inspection of images show the increase in vegetation cover between 1999 and 2006.

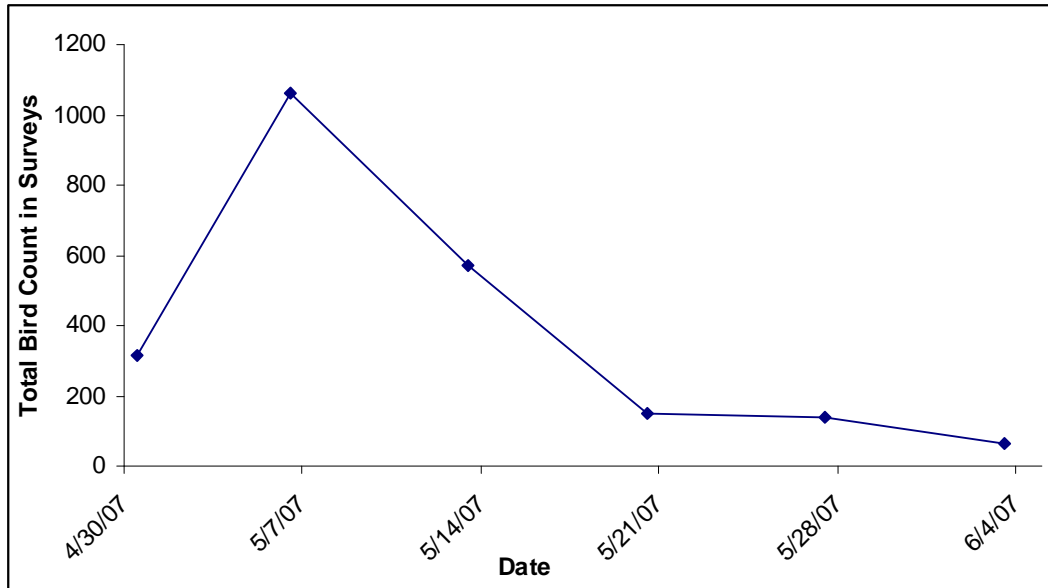


Figure 3. Total number of Semipalmated Sandpipers counted at 39 survey points (3 in each of 13 managed wetland units) at the Tom Yawkey Wildlife Center, South Carolina during Spring migration 2007. Surveys were conducted on April 30th, May 6th, May 13th, May 20th, May 27th, and June 3rd. A total of 9.42 ha were surveyed in clusters 1 and 2 each period, and a total of 37.70 ha were surveyed in cluster 3 each period.

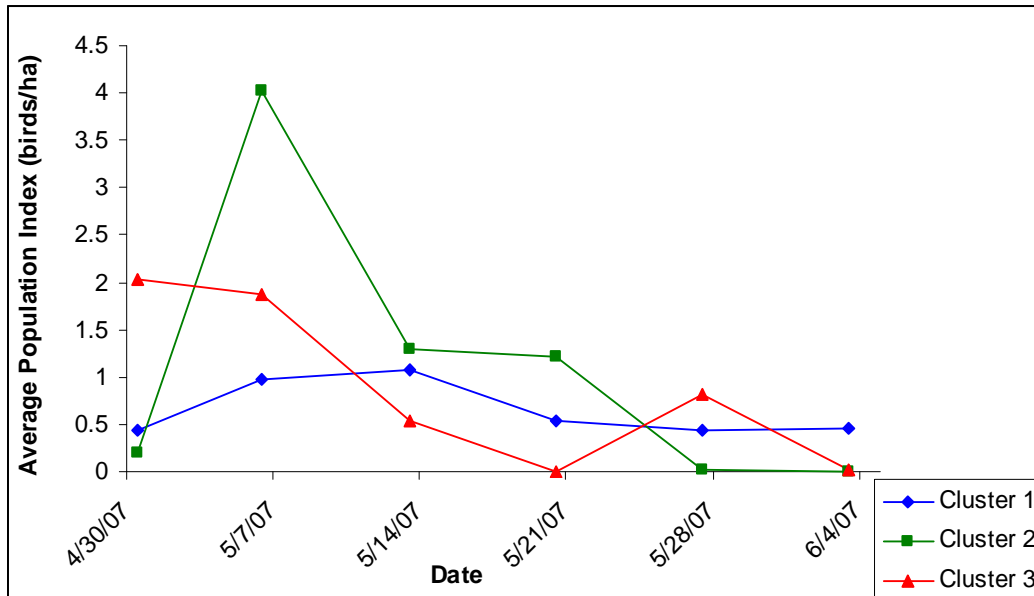
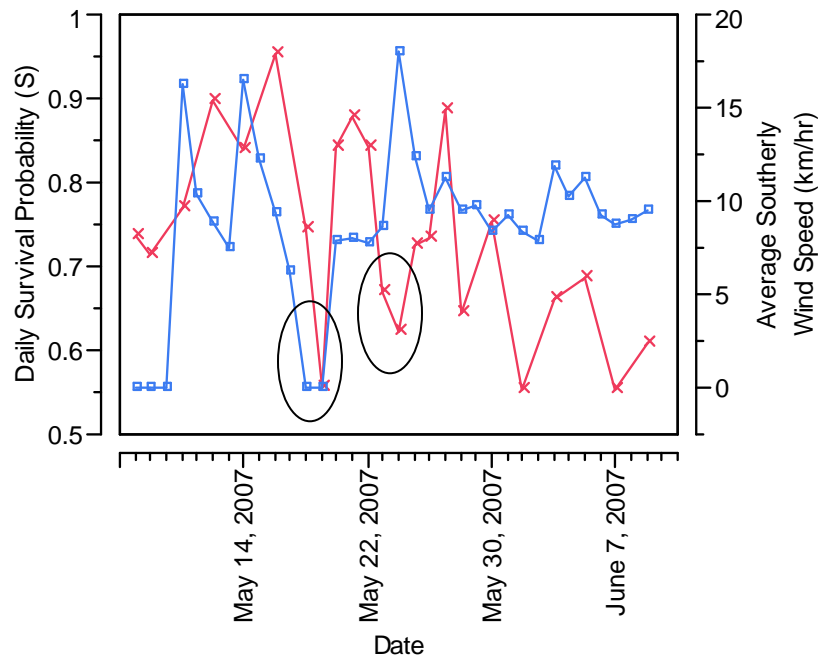


Figure 4. Average weekly estimate of Semipalmated Sandpipers per hectare (ha) in each cluster of managed wetland units at the Tom Yawkey Wildlife Refuge, South Carolina during spring migration in 2007. Surveys were conducted on April 30th, May 6th, May 13th, May 20th, May 27th, and June 3rd. A total of 9.42 ha were surveyed in clusters 1 and 2 each period, and a total of 37.70 ha were surveyed in cluster 3 each period.



Left Scale: x — Daily Survival Probability (S)

Right Scale: □ — Average Southerly Wind Speed (km/hr)

Figure 5. Residency rates (i.e., daily survival probability, \hat{S}) of Semipalmated Sandpipers and average daily southerly wind speeds at the Tom Yawkey Wildlife Center, South Carolina, Spring 2007. May 20th (first oval) illustrates an event of low residency (high departure) and low wind speed after a period of decreasing wind speed. Meanwhile May 24th and 25th (second oval) illustrates an event of low residency corresponding to days of higher wind speed.

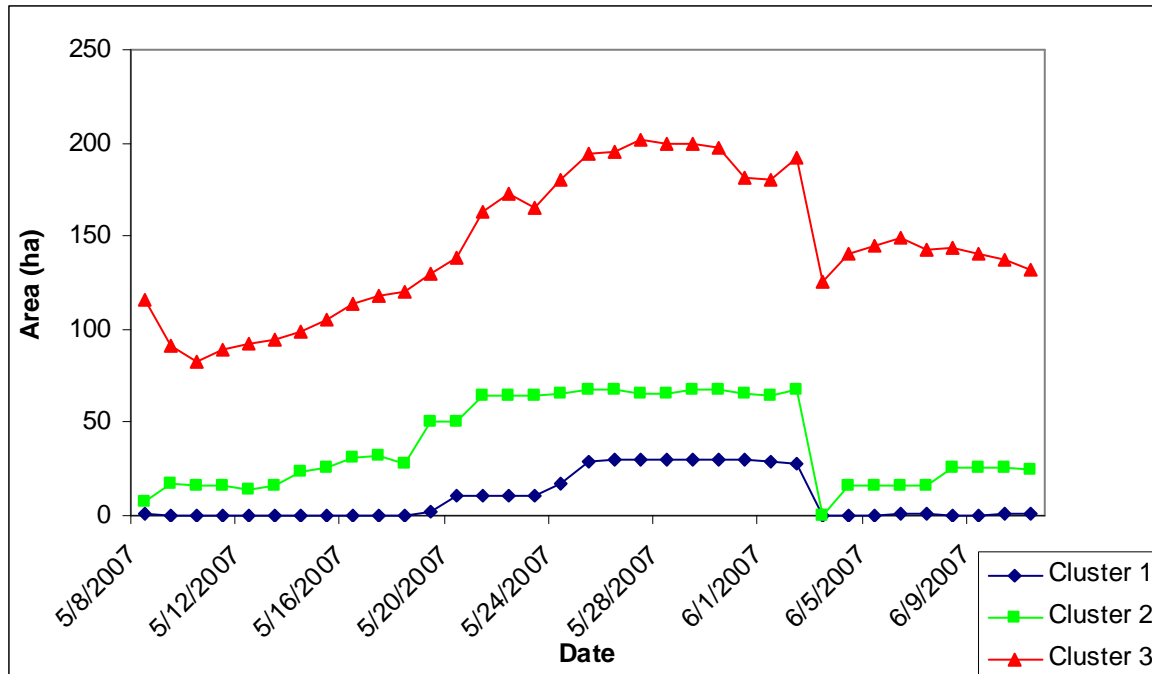


Figure 6. Total amount of accessible habitat (ha) in three clusters of managed wetland units at the Tom Yawkey Wildlife Center, South Carolina during Spring migration of Semipalmated Sandpipers in 2007. Cluster 3 had the greatest number of managed wetland units (n=8) and area (286 ha). Clusters 1 (48 ha) and 2 (83 ha) had two managed wetland units each. A fast draw down was implemented on 17 May 2007. The marked decrease in accessible habitat on June 2 and 3 in 2007 was caused by a rainfall event of ~6.35 cm.

Table 2. Model selection for residency rates of Semipalmated Sandpipers at the Tom Yawkey Wildlife Center, South Carolina, Spring 2006. Model parameters include ΔQAICc values (median $\hat{c} = 1.02$), QAICc weights, QDeviance and number of model parameters. Residency (S) and resighting probabilities (p) were modeled as either constant (.) or variable with respect to time using reduced parameter models. Time-varying models were also modeled with a linear (T) or quadratic (TT) term. Three covariates were used to model residency rates: estimated percent fat (epf) and southerly wind speed (Swind). Covariates and interaction (*) between epf and Swind covariates were modeled as additive effects (+).

Model	Delta QAICc	QAICc Weight	#Par	QDeviance
{S(TT+epf+Swind+epf*Swind) p(.) }	0	0.46963	7	1079.662
{S(TT+epf+Swind p(.) }	1.74	0.1971	6	1083.445
{S(epf+Swind+epf*Swind) p(.) }	2.17	0.15831	5	1085.922
{S(TT+epf) p(.) }	4.77	0.04325	5	1088.517
{S(t) p(.) }	4.96	0.03943	21	1055.262
{S(epf) p(.) }	5.88	0.0248	3	1093.688
{S(TT) p(.) }	6.48	0.01835	4	1092.265
{S(epf) p(T) }	6.64	0.01702	4	1092.415
{S(.) p(.) }	7.36	0.01185	2	1097.184
{S(TT+epf+epf*TT) p(.) }	8.05	0.00838	7	1087.714
{S(T) p(.) }	8.99	0.00525	3	1096.793
{S(.) p(T) }	9.19	0.00474	3	1096.999
{S(T) p(T) }	11.01	0.00191	4	1096.789

Table 3. Beta parameter estimates for the top model of residency (\hat{S}) and detection probability (\hat{p}) of Semipalmated Sandpipers at the Yawkey Wildlife Center, South Carolina, Spring 2006. Covariates were modeled as additive effects on time-varying, reduced parameter models. Additive effects included the interaction between estimated percent fat (epf) and southerly wind speed (Swind).

Model Term	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
<u>Daily Survival</u> (\hat{S})				
Intercept	1.51417	1.28704	-1.00843	4.03678
T (linear)	0.07034	0.12018	-0.16521	0.30589
TT (curvilinear)	-0.00680	0.00593	-0.01843	0.00483
Epf	0.13192	0.05085	0.03225	0.23159
Swind	-0.07357	0.16623	-0.39938	0.25223
Epf*Swind	-0.01774	0.00781	-0.03305	-0.00243
<u>Detection</u> (\hat{p})				
Constant	-2.41388	0.14481	-2.69771	-2.13005

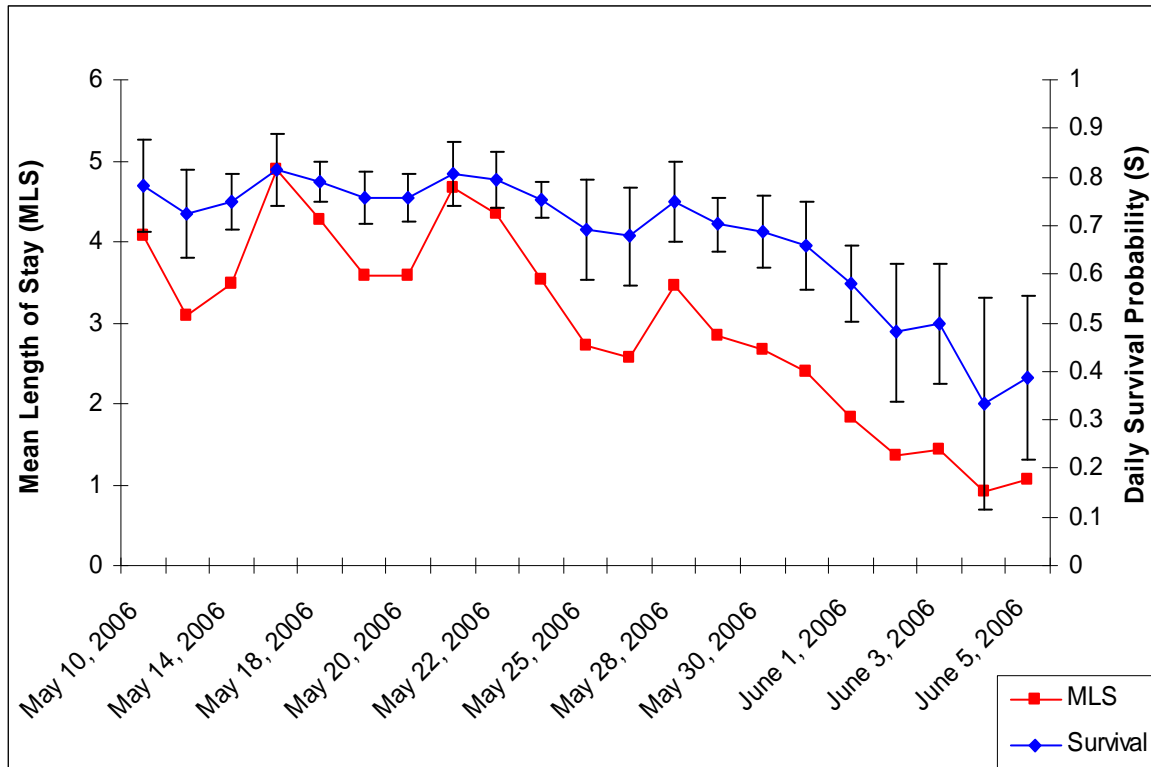


Figure 7. Residency rates (i.e., daily survival probability, \hat{S}) and mean length of stay (MLS) of Semipalmated Sandpipers at the Tom Yawkey Wildlife Center, South Carolina, Spring 2006. The 95% confidence intervals for residency rates are depicted.

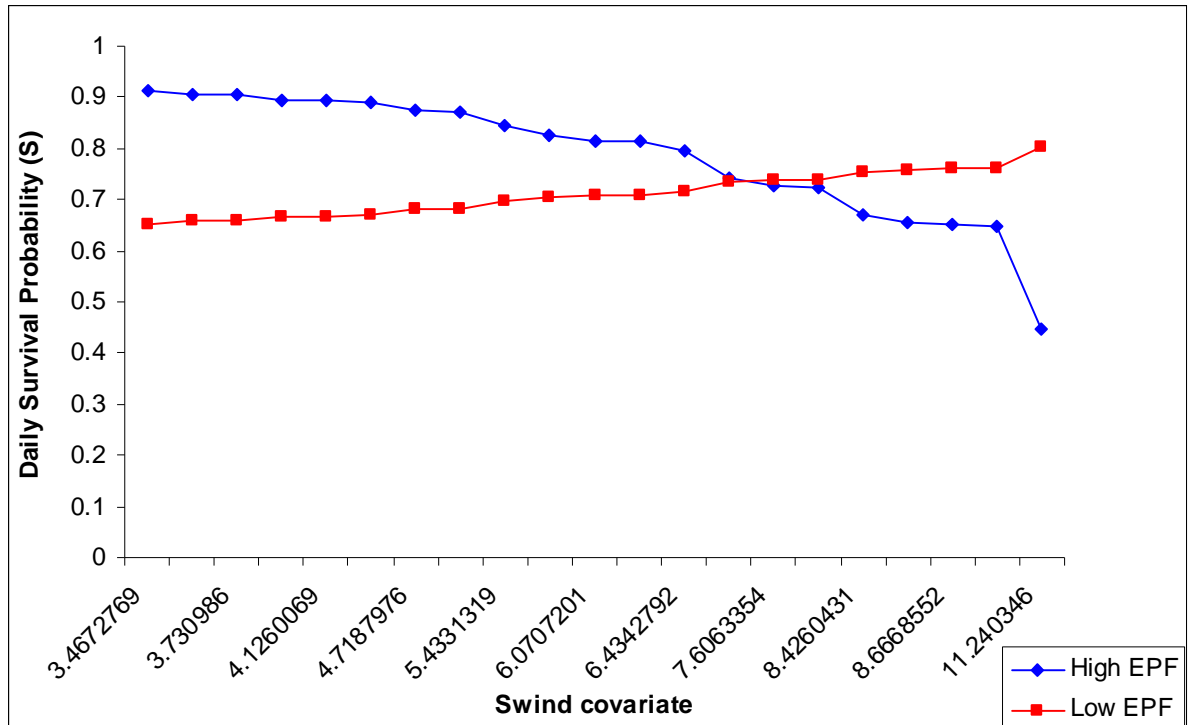


Figure 8. Predicted pattern of residency rates (i.e., daily survival probability, \hat{S}) of Semipalmated Sandpipers at the Tom Yawkey Wildlife Center, South Carolina resulting from the interaction between Swind and epf during Spring migration 2006. The high epf value used was the average of epf values greater than zero (14.47). The low epf value was the average of epf values less than zero (-9.84). As the southerly wind increases, the difference in residency rates between high and low epf values is minimized.

Table 4. Model selection for residency rates of Semipalmated Sandpipers at the Tom Yawkey Wildlife Center, South Carolina, Spring 2007. Model parameters include ΔQAICc values (median $\hat{c} = 1.187$), QAICc weights, Qdeviance and number of model parameters. Residency (S) was modeled as either constant (.) or variable with respect to time using reduced parameter models. Two covariates were used to model residency rates: estimated percent fat (epf) and southerly wind speed (Swind). Encounter probabilities (p) were modeled as constant (.), time variable (t) or by group (i.e., resight, telemetry). Time-varying models were also modeled with a linear (T) or quadratic (TT) term. Covariates and the interaction between epf and Swind (*) were modeled as additive effects (+). Only models with a $\Delta\text{QAICc} \leq 10$ are listed.

Model	Delta QAICc	QAICc Weight	#Par	QDeviance
{S(T+epf+Swind+Swind*epf) p(g) }	0	0.61521	7	1694.638
{S(T+epf+Swind) p(g) }	1.56	0.28204	6	1698.229
{S(T+Swind) p(g) }	4.99	0.05085	5	1703.682
{S(T+epf+T*epf) p(g) }	7.1	0.01771	6	1703.765
{S(t) p(g) }	7.3	0.01599	25	1664.588
{S(T) p(g) }	7.94	0.01159	4	1708.662
{S(TT) p(g) }	9.76	0.00467	5	1708.456

Table 5. Beta parameter estimates for the top residency model (\hat{S}) and detection probability (\hat{p}) of Semipalmated Sandpipers at the Yawkey Wildlife Center, South Carolina, Spring 2007. Covariates were modeled as additive effects on time-varying, reduced parameter models. Additive effects included the interaction between estimated percent fat (epf) and southerly wind speed (Swind).

Model Term	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
<u>Daily Survival</u> (\hat{S})				
Intercept	1.15312	0.32288	0.52026	1.78597
T (linear)	-0.12469	0.03219	-0.18779	-0.06159
Epf	0.05458	0.02014	0.01510	0.09406
Swind	0.29552	0.09726	0.10489	0.48617
Epf*Swind	-0.00887	0.00448	-0.01765	-0.00009
<u>Detection</u> (\hat{p})				
Intercept (resight)	0.85733	0.14863	0.56602	1.14864
Telemetry	-2.91720	0.19429	-3.29801	-2.53639

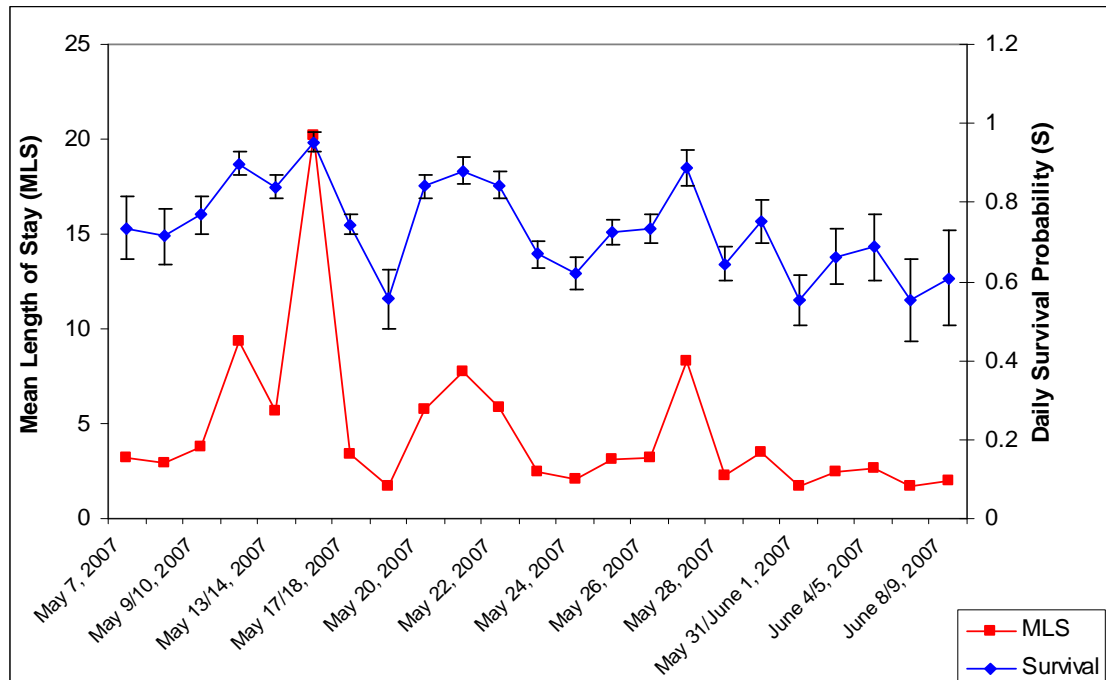


Figure 9. Residency rates (i.e., daily survival probability, \hat{S}) and mean length of stay (MLS) of Semipalmated Sandpipers at the Tom Yawkey Wildlife Center, South Carolina, Spring 2007. The 95% confidence intervals for residency rates are depicted.

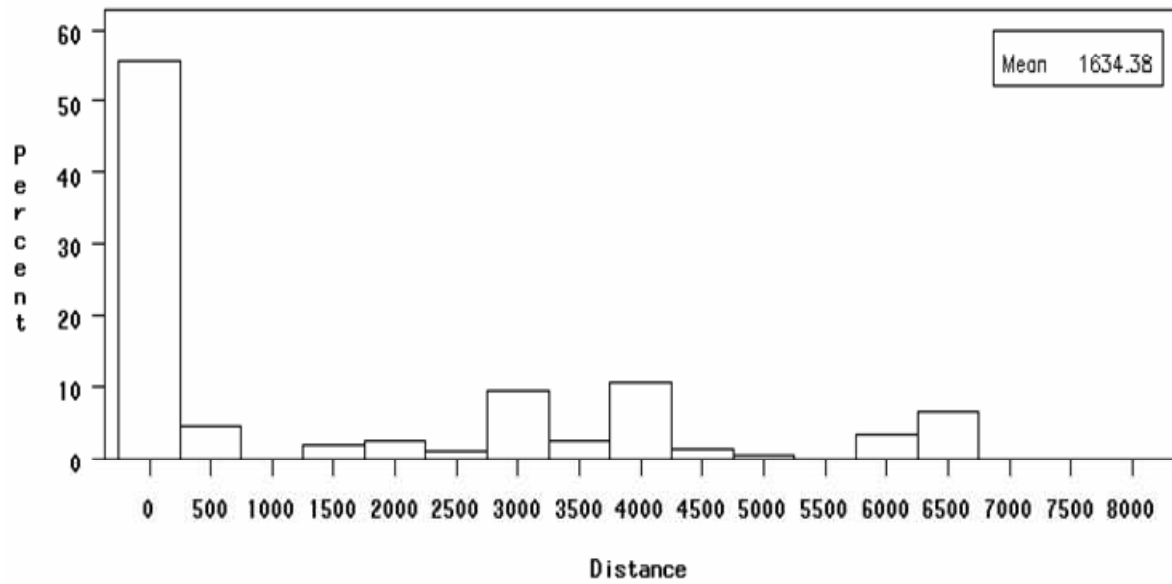


Figure 10. Farthest distance traveled by various proportions of Semipalmated Sandpipers from their original banding site at the Tom Yawkey Wildlife Center, South Carolina, Spring 2007. The average maximum distance traveled by marked Semipalmated Sandpipers from their banding site was 1634 m.

Table 6. Model selection for residency (S) and movement rates (Psi, ψ) of Semipalmated Sandpipers among wetland clusters at the Tom Yawkey Wildlife Center, South Carolina, Spring 2007. Model parameters include Δ AICc values, AICc weights, number of model parameters, and deviance. Seven covariates were used to model residency and movement rates: estimated percent fat (epf), southerly wind speed (Swind), prey biomass (prey), index of bird density (bird), proportion of accessible habitat per cluster (access), total area in the cluster of interest (area), and nearest-neighbor inter-cluster distance (distance). These covariates were modeled as additive effects on either constant or time-varying residency and movement rates models using reduced parameter models. Time-varying models were also modeled with an additive linear (T) or quadratic (TT) term. Encounter probabilities (p) were modeled as constant (.), time varying (*t*) or by group (i.e., resight or telemetry). Covariates and interactions (*) between epf and Swind, and prey and access were modeled as additive effects (+). Only models with a Δ AICc ≤ 10 are listed.

Model	Delta AICc	AICc Weight	#Par	Deviance
{S (TT+epf+prey+access+Swind+epf*Swind+prey*access), p (g+Area), Psi (cluster+TT+bird+distance)}	0	0.45634	19	2351.343
{S (T+epf+prey+access+Swind+epf*Swind+prey*access), p (g+Area), Psi (cluster+T+bird+distance)}	0.67	0.32707	17	2356.177
{S (TT+epf+prey+access+Swind+epf*Swind+prey*access+bird), p (g+Area), Psi (cluster+TT+bird+distance)}	2.05	0.16345	20	2351.305
{S (TT+epf+Swind+epf*Swind), p (g+Area), Psi (cluster+TT+bird+distance)}	5.3	0.03224	16	2362.888
{S (TT+prey+access+prey*access), p (g+Area), Psi (TT+bird+distance)}	6.71	0.0159	16	2364.302
{S (TT+epf+Swind+Swind*epf), p (g+Area), Psi (TT+access+prey+prey*access+bird+distance)}	9.08	0.00487	19	2360.421

Table 7. Beta parameter estimates for the inter-cluster top model of residency (\hat{S}), detection (\hat{p}), and movement probabilities ($\hat{\psi}$) of Semipalmated Sandpipers at the Yawkey Wildlife Center, South Carolina, Spring 2007. Covariates were modeled as additive effects on time-varying, reduced parameter models. Additive effects included the interaction (*) between estimated percent fat (epf) and southerly wind speed (Swind), and prey biomass (prey) and relative proportion of accessible habitat (depth 0-4 cm; access) among three wetland clusters.

Model Term	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
<u>Daily Survival (\hat{S})</u>				
Intercept	0.20625	0.78967	-1.34149	1.75400
T (linear)	-0.03446	0.10456	-0.23933	0.17041
TT (curvilinear)	-0.00393	0.00410	-0.01197	0.00411
Ep _f	0.05677	0.01984	0.01781	0.09559
Prey	0.14885	0.10920	-0.06517	0.36289
Access	5.26068	2.98809	-0.59598	11.11734
Swind	0.23211	0.09505	0.04579	0.41842
Ep _f *Swind	-0.00879	0.00430	-0.01723	-0.00036
Prey*Access	-0.53660	0.27717	-1.07986	0.00665
<u>Detection (\hat{p})</u>				
Intercept (telemetry)	0.59422	0.23934	0.12510	1.06334
Resight	-2.98729	0.18470	-3.33493	-2.62528
Area	0.00134	0.00100	-0.00062	0.00331
<u>Daily Movement ($\hat{\psi}$)</u>				
Intercept (Cluster 1)	3.40819	1.37905	0.70525	6.11113
Cluster 2	2.50846	0.34922	1.82399	3.19293
Cluster 3	-0.59462	0.33237	-1.24607	0.05682
T (linear)	-0.30213	0.11697	-0.53141	-0.07285
TT (curvilinear)	0.01066	0.00533	0.00021	0.02111
Birds	-1.90017	0.38627	-2.65728	-1.14309
Distance	-1.59546	0.40391	-2.38712	-0.80380

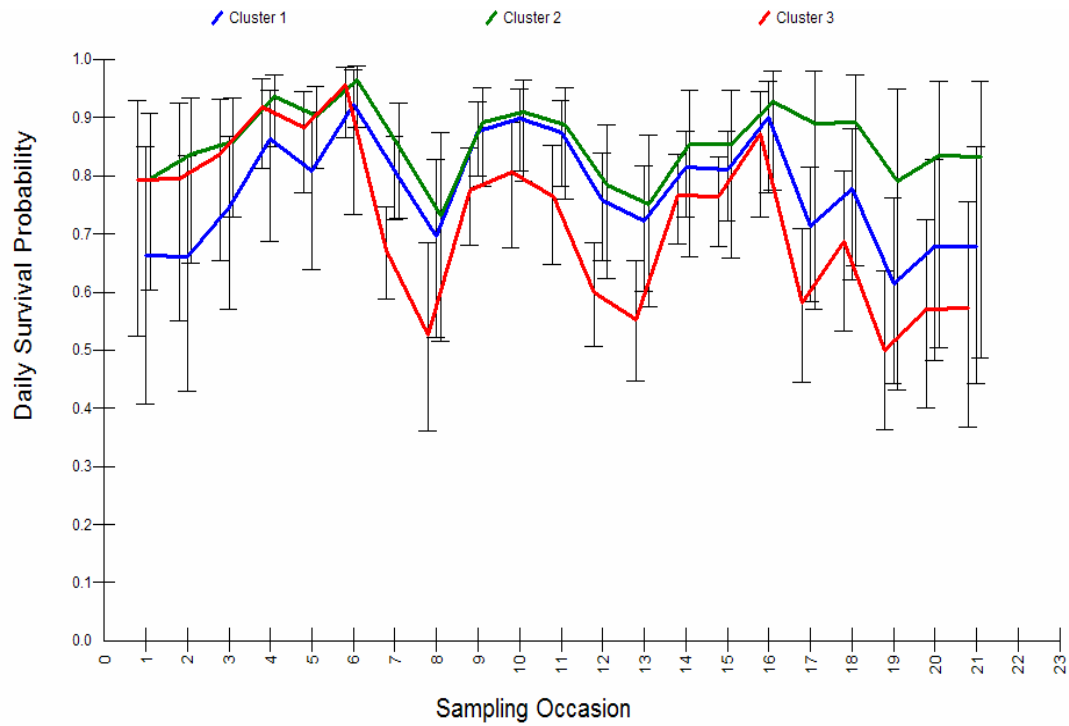


Figure 11. Residency rates (i.e., daily survival probability, \hat{S}) and 95% confidence intervals of Semipalmated Sandpipers at each of three clusters at the Tom Yawkey Wildlife Center, South Carolina during Spring 2007. The first sampling occasion was May 8th and the last on June 11th. The blue line depicts daily residency rates for birds banded in cluster 1, the green line for birds banded in cluster 2, and the red line depicts for birds banded in cluster 3.

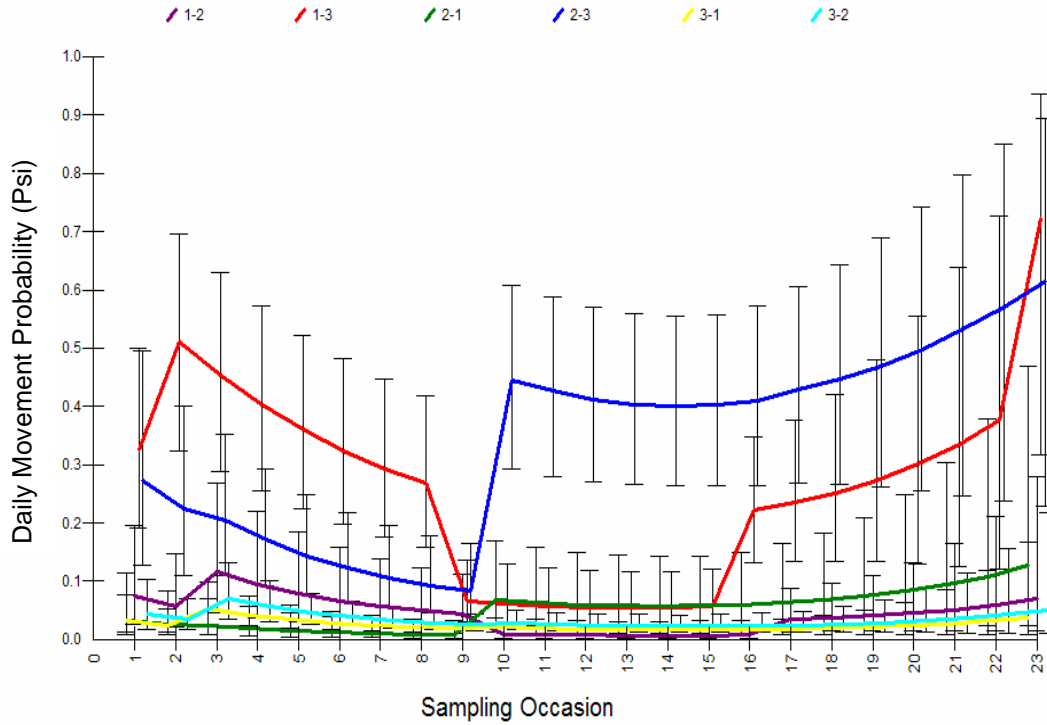


Figure 12. Daily movement rates (Φ , $\hat{\psi}$) and 95% confidence intervals of Semipalmated Sandpipers among three wetland clusters at the Tom Yawkey Wildlife Center, South Carolina during Spring 2007. The first sampling occasion was May 8th and the last on June 11th. The blue line depicts the movement probability cluster 2 to cluster 3; the red line depicts the movement probability from cluster 1 to cluster 3; all other movement rates were negligible.

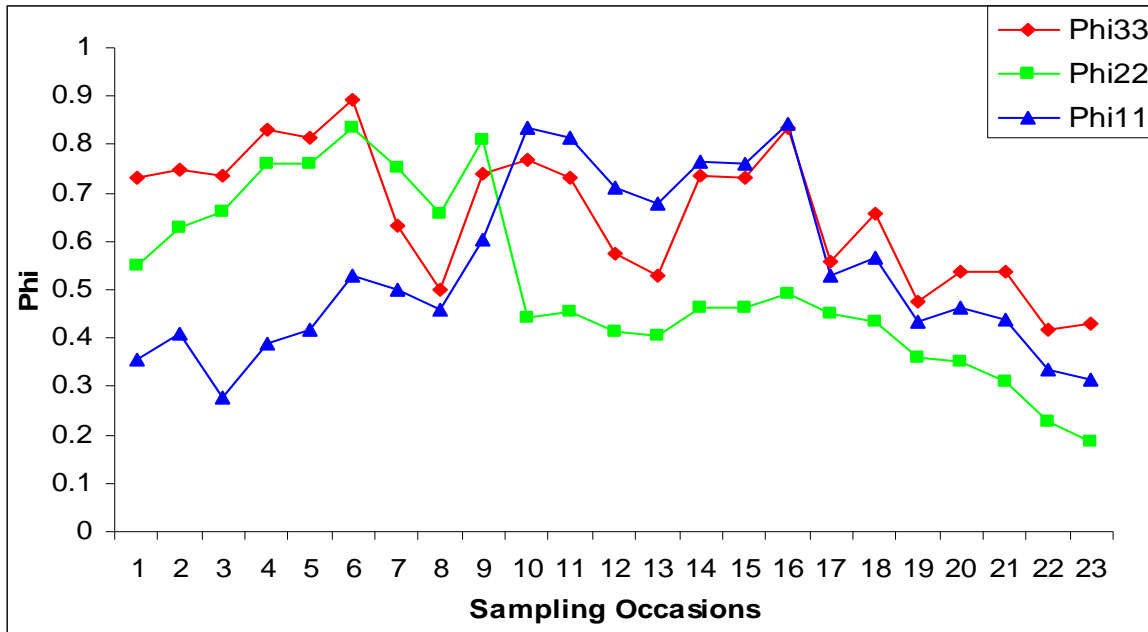


Figure 13. Seasonal patterns of the probability of surviving and staying at a cluster 1 (Φ_{11} , $\hat{\Phi}^{11}$), cluster 2 (Φ_{22} , $\hat{\Phi}^{22}$), and cluster 3 (Φ_{33} , $\hat{\Phi}^{33}$) by Semipalmated Sandpipers at the Yawkey Wildlife Center, South Carolina during Spring 2007. The first sampling occasion was May 8th and the last was on June 11th.

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Appendices

Appendix I. List of invertebrate taxa detected (present/absent) in each of three wetland clusters at The Tom Yawkey Wildlife Center, South Carolina, Spring 2006 and 2007. Summary includes average prey biomass (mg/cm³) by sampled substrate (mud or water column) and combined (all taxa, all substrates). Average prey biomass by substrate or combined and cluster were compared using ANOVA. Statistical differences ($p < 0.05$) between any pair of cluster are indicated by an asterisk. Presence in the sample is denoted by 1; absence by 0.

2006 Invertebrate Sampling Summary

	Presence/Absence			Mud Density			Water Density			Combined Mud and Water Density		
	Cluster 1	Cluster 2	Cluster 3	Cluster 1	Cluster 2	Cluster 3	Cluster 1	Cluster 2	Cluster 3	Cluster 1	Cluster 2	Cluster 3
Polychaeta	1	1	1	0.000369	0.011688	0.026877	0.000007	0.000935	0.000187	0.000377	0.012623	0.027064
Chironomidae	1	1	1	0.004196	0.000232	0.003034	0.000279	0.000169	0.000072	0.004475*	0.000401	0.003106
Oligochaeta	0	1	0	0	0	0	0	0.000001	0	0	0.000001	0
Diptera	0	1	1	0	0.000548	0.000168	0	0	0	0	0.000548	0.000168
Amphipoda	0	0	1	0	0	0.002160	0	0	0.002603	0	0	0.004763
Odonata	0	1	0	0	0	0.000000	0	0.000021	0	0	0.000021	0
Gastropod	1	1	1	0	0	0.010317	0.000016	0.000105	0.000314	0.000016	0.000105	0.010631
Corixidae	1	0	1	0	0	0.000238	0.000396	0	0.003236	0.000396	0	0.003473
Coleoptera	0	0	0	0	0	0.000000	0	0	0	0	0	0
Trichoptera	1	0	0	0	0	0.000000	0.000252	0	0	0.000252*	0	0

2007 Invertebrate Sampling Summary

	Presence/Absence			Mud Density			Water Density			Combined Mud and Water Density		
	Cluster 1	Cluster 2	Cluster 3	Cluster 1	Cluster 2	Cluster 3	Cluster 1	Cluster 2	Cluster 3	Cluster 1	Cluster 2	Cluster 3
Polychaeta	1	1	1	0.013417	0.005533	0.069184	0.000905	0.000131	0.002191	0.014322	0.005664	0.071375
Chironomidae	1	1	1	0.006980	0.000026	0.018429	0.001054	0.000035	0.005419	0.008034	0.000061	0.023847
Oligochaeta	1	0	1	0.001403	0	0.001286	0.000040	0	0.000017	0.001443	0*	0.001303
Diptera	1	0	1	0.000022	0	0.000209	0.000053	0.000000	0.000058	0.000075	0	0.000268
Amphipoda	1	0	1	0.000173	0	0.143879	0	0.008930	0.000913	0.000173	0.008930	0.144792
Odonata	1	0	1	0.000154	0	0	0.000009	0	0.000923	0.000164	0	0.000923
Gastropod	1	1	1	0.000988	0.010897	0.071095	0.002700	0.001735	0.071870	0.003688	0.012632	0.142964
Corixidae	1	1	1	0.002076	0	0	0.002642	0.000038	0.004110	0.004717	0.000038*	0.004110
Coleoptera	1	0	0	0.000118	0	0	0	0	0	0.000118	0	0
Trichoptera	1	0	0	0.000367	0	0	0	0	0	0.000367	0	0

Appendix II. List of *a priori* models used to assess daily residency (\hat{S}) and movement ($\hat{\psi}$) rates among wetland clusters of Semipalmated Sandpipers at the Tom Yawkey Wildlife Center, South Carolina, Spring 2007.

Naïve, Area and Distance Models – Constant S and Psi, Constant p

$$\begin{aligned} S^{(.)} p^{(.)} \psi^{(.)} \\ S^{(.)} p_{\text{cluster}} \psi_{\text{cluster}} \\ S_{\text{cluster}} p^{(.)} \psi_{\text{cluster}} \\ S_{\text{cluster}} p_{\text{cluster}} \psi^{(.)} \\ S_{\text{cluster}} p_{\text{cluster}} \psi_{\text{cluster}} \\ S_{\text{cluster}} p_{\text{Area}} \psi_{\text{cluster}} \\ S_{\text{cluster}} p_{\text{cluster}} \psi_{\text{distance}} \\ S_{\text{Area}} p_{\text{cluster}} \psi_{\text{distance}} \\ S_{\text{cluster}} p_{\text{Area}} \psi_{\text{distance}} \end{aligned}$$

Area and Distance Models – Constant S and Psi, p by group (i.e., Resight and Telemetry)

$$\begin{aligned} S_{\text{cluster}} p^{(g)} \psi_{\text{cluster}} \\ S_{\text{cluster}} p^{(g)} \psi_{\text{distance}} \\ S_{\text{Area}} p^{(g)} \psi_{\text{cluster}} \\ S_{\text{Area}} p^{(g)} \psi_{\text{distance}} \\ S_{\text{cluster}} p^{(g)} \psi_{\text{Area}} \\ S_{\text{cluster}} p^{(g+\text{area})} \psi_{\text{cluster}} \\ S_{\text{cluster}} p^{(g+\text{area})} \psi_{\text{distance}} \\ S_{\text{cluster}} p^{(g+\text{area})} \psi_{\text{Area}} \end{aligned}$$

Time-varying Models (epf, prey, Swind, access, birds, distance)

$$\begin{aligned} S^{\text{TT}+\text{access}} p^{g+\text{Area}} \psi_{\text{cluster}+\text{distance}} \\ S^{\text{TT}+\text{birds}} p^{g+\text{Area}} \psi_{\text{cluster}+\text{distance}} \\ S^{\text{TT}+\text{prey}} p^{g+\text{Area}} \psi_{\text{cluster}+\text{distance}} \\ S^{\text{TT}+\text{Swind}} p^{g+\text{Area}} \psi_{\text{cluster}+\text{distance}} \\ S^{\text{TT}+\text{prey}+\text{access}+\text{prey}*\text{access}} p^{g+\text{Area}} \psi_{\text{cluster}+\text{distance}} \\ S^{\text{TT}+\text{epf}+\text{Swind}+\text{epf}*\text{Swind}} p^{g+\text{Area}} \psi_{\text{cluster}+\text{distance}} \end{aligned}$$

$$\begin{aligned} S^{\text{T}+\text{cluster}} p^g \psi^{\text{T}+\text{cluster}} \\ S^{\text{TT}+\text{cluster}} p^g \psi^{\text{TT}+\text{cluster}} \end{aligned}$$

$$\begin{aligned} S^{\text{TT}+\text{access}} p^{g+\text{Area}} \psi_{\text{cluster}+\text{TT}+\text{access}} \\ S^{\text{TT}+\text{access}} p^{g+\text{Area}} \psi_{\text{cluster}+\text{TT}+\text{birds}} \\ S^{\text{TT}+\text{access}} p^{g+\text{Area}} \psi_{\text{cluster}+\text{TT}+\text{prey}} \\ S^{\text{TT}+\text{birds}} p^{g+\text{Area}} \psi_{\text{cluster}+\text{TT}+\text{access}} \\ S^{\text{TT}+\text{birds}} p^{g+\text{Area}} \psi_{\text{cluster}+\text{TT}+\text{birds}} \\ S^{\text{TT}+\text{birds}} p^{g+\text{Area}} \psi_{\text{cluster}+\text{TT}+\text{prey}} \end{aligned}$$

$$\begin{aligned}
S^{TT+prey} p^{g+Area} \Psi^{cluster+TT+access} \\
S^{TT+prey} p^{g+Area} \Psi^{cluster+TT+birds} \\
S^{TT+prey} p^{g+Area} \Psi^{cluster+TT+prey} \\
S^{TT+Swind} p^{g+Area} \Psi^{cluster+TT+access} \\
S^{TT+Swind} p^{g+Area} \Psi^{cluster+TT+birds} \\
S^{TT+Swind} p^{g+Area} \Psi^{cluster+TT+prey}
\end{aligned}$$

$$\begin{aligned}
S^{TT+epf+Swind+epf*Swind} p^{g+Area} \Psi^{cluster+TT+access} \\
S^{TT+epf+Swind+epf*Swind} p^{g+Area} \Psi^{cluster+TT+birds} \\
S^{TT+epf+Swind+epf*Swind} p^{g+Area} \Psi^{cluster+TT+prey} \\
S^{TT+epf+Swind+epf*Swind} p^{g+Area} \Psi^{cluster+TT+birds+distance} \\
S^{TT+epf+Swind+epf*Swind} p^{g+Area} \Psi^{cluster+TT+prey+distance} \\
S^{TT+epf+Swind+epf*Swind} p^{g+Area} \Psi^{cluster+TT+prey+access+distance} \\
S^{TT+epf+Swind+epf*Swind} p^{g+Area} \Psi^{TT+access+prey+prey*access+distance} \\
S^{TT+epf+Swind+epf*Swind} p^{g+Area} \Psi^{TT+access+prey+prey*access+birds+distance}
\end{aligned}$$

$$\begin{aligned}
S^{TT+prey+access+prey*access} p^{g+Area} \Psi^{cluster+TT+birds+distance} \\
S^{TT+prey+access+prey*access} p^{g+Area} \Psi^{cluster+TT+prey+access+prey*access} \\
S^{TT+prey+access+prey*access} p^{g+Area} \Psi^{cluster+TT+prey+access+prey*access+birds} \\
S^{TT+prey+access+prey*access} p^{g+Area} \Psi^{cluster+TT+prey+access+prey*access+distance}
\end{aligned}$$

$$\begin{aligned}
S^{epf+Swind+epf*Swind+prey+access+prey*access} p^{g+Area} \Psi^{cluster+birds+distance} \\
S^{T+epf+Swind+epf*Swind+prey+access+prey*access} p^{g+Area} \Psi^{cluster+T+birds+distance} \\
S^{TT+epf+Swind+epf*Swind+prey+access+prey*access} p^{g+Area} \Psi^{cluster+TT+birds} \\
S^{TT+epf+Swind+epf*Swind+prey+access+prey*access} p^{g+Area} \Psi^{cluster+TT+birds+distance} \\
S^{TT+epf+Swind+epf*Swind+prey+access+prey*access+birds} p^{g+Area} \Psi^{cluster+TT+birds+distance}
\end{aligned}$$

CHAPTER 2

Introduction

The US Shorebird Conservation Plan calls for creating sufficient suitable habitat for migrant shorebirds to enhance their ability to meet migratory and pre-breeding energetic requirements (Brown et al. 2001). Sufficient habitat is defined as the number of accessible hectares required to meet those needs given prey levels and mean length of stay (Loesch et al. 1995). Numerous studies have determined that small shorebirds are selectively attracted to sites with shallow water (0-4 cm) and exposed mudflats (Weber and Haig 1996, Davis and Smith 1998, Collazo et al. 2002). One mechanism available to managers to create accessible habitat is to implement water drawdowns. Upon exposing newly available habitat, shorebirds can rapidly respond by arriving in the new habitat in as little as 4 to 24 hours (Rundle and Fredrickson 1981).

Few studies have experimentally manipulated managed wetlands utilizing various drawdown regimes to assess the benefits accrued from such practices. Early work on this subject was conducted by Rundle and Fredrickson (1981). They reported that a gradual drawdown was more effective than a rapid one at attracting shorebirds, as a rapid drawdown quickly produced dried mudflats and hard-pans. It is worth noting that in their study a drawdown was defined as a “total dewatering of the unit” instead of a drawdown scheme to maximize the extent of desired water levels (Collazo et al. 2002). Parsons (2002) studied multiple drawdown patterns in streams in the Delaware Bay estuary. Her results showed that shorebirds were most abundant at impounded sites with lowest water depths, but her work did not explicitly address the advantages of different drawdown rates. In 2005 the US Fish

and Wildlife Service completed a project in the northeastern United States assessing the numeric response of shorebirds to two hydrologic regimes during the spring migration season (M. Runge, Patuxent Wildl. Res. Ctr, pers. comm.). The regimes were a slow, gradual drawdown and a fast drawdown. The latter maximized the amount of accessible habitat at the time of peak influx of migrants during the season. Preliminary results suggest that, in most instances, shorebirds used newly available areas, presumably accommodating new arrivals (M. Runge, unpubl. data).

From the above referenced studies it is clear that there can be a numeric response to rapid drawdowns; however, there have been no explicit tests designed to quantify if the initial numeric response is followed by a behavioral, functional response (*sensu* Goodwin 2003, Belisle 2005). Movement and residency decisions of shorebirds reflect the quality of habitat, and thus, residency in- and movement to- rapid drawdown management units are expressions of a functional response to management actions. Given that the primary purpose of either management practice is to help shorebirds meet their energetic requirements, establishing the added value of a rapid drawdown is important to strengthen the rationale advocating its continued use. Conversely, some refuges might not have the capability to implement a rapid drawdown (e.g., culverts capped on one end) or opt not to implement one because it might interfere with other non-shorebird management priorities. It is, therefore, also important to determine shorebird responses to assess management tradeoffs, options and their conservation value.

To address this question, I hypothesized that birds would quickly move to and remain at newly exposed habitat created by a rapid drawdown. Movement and residency probabilities would reflect decisions made by shorebirds to take advantage of conditions that

facilitate maximizing prey intake. This would mean not only that new arrivals would remain in wetland units managed under a fast drawdown regime, but that birds present in neighboring wetland units managed differently would redistribute themselves to take advantage of newly exposed resources. The biological underpinnings of my hypothesis were twofold. First, site quality can be influenced by the extent of accessible habitat and the prey base it makes available to shorebirds (Hicklin and Smith 1984, Farmer and Wiens 1999, Collazo et al. 2002, Ydenberg et al. 2002, Pomeroy 2006). Second, augmenting accessible habitat via fast drawdowns would be more effective if fast managed units occurred in close proximity to slow-managed units. In doing so, a functionally connected patchwork of resource options is increased. Such a landscape lessens the importance of inter-managed unit distance in favor of foraging decisions based on prey distribution at smaller scales (Hicklin and Smith 1984, Farmer and Wiens 1999, Belisle 2005).

In 2006 and 2007, I conducted management experiments in 13 managed wetland units to estimate residency and movement rates of Semipalmated Sandpipers (*Calidris pusilla*) under slow and fast drawdown regimes. The experiments were conducted at the Tom Yawkey Wildlife Center, South Carolina. Estimates were obtained using multi-state models (Kendall and Nichols 2004). Residency rates (S) were defined as the probability that a bird, banded at treatment j on day i , remains at YWC to day $i+1$. Movement rates (Ψ) were defined as the probability that a bird, banded in treatment j on day i , moves to another treatment on day $i+1$. Each year, the slow drawdown was begun prior to the arrival of Semipalmated Sandpipers to ensure the availability of accessible habitat throughout the season. The fast drawdown was initiated May 17th in anticipation of the peak of migration which typically occurs on May 20th (Lyons and Haig 1995, Weber and Haig 1996).

In concert with my hypothesis, I predicted that movements to units under a fast treatment would increase post-treatment and that residency rates at such units would significantly exceed residency rates recorded at neighboring, slow-managed units for the remainder of the season. These predictions were predicated on the fact that the proportion of newly exposed habitat in slow-managed units becomes increasingly smaller as the season progresses. In contrast, the proportion and quality of newly exposed habitat in fast-managed units is expected to be greater as the full extent of it becomes accessible nearly all at once. Moreover, the prey quality of previously exposed habitat should be diminished by shorebird predation and as it dries out (Rundle and Fredrickson 1981, Schneider and Harrington 1981, Hicklin and Smith 1984).

I modeled shorebird residency and movement rates as a function of prey biomass (mg/cm^3) and the relative proportion of accessible habitat (ha) over the migratory season to ascertain linkages of responses with management actions. I also modeled estimated percent fat, southerly wind speed, an index of shorebird density, and the average distance to the nearest treatment (proximity). Epf and southerly winds were included because these factors influence the number and duration of stops made by migrant shorebirds (Dunn et al. 1988, Butler et al. 1997, Farmer and Wiens 1999, Åkesson and Hedenström 2000, Hostetler 2004, Chapter 1). Moreover, epf provides a plausible link between site quality, influenced by management, and residency rates (Lyons and Collazo in Press). Shorebird density was included because feeding flocks may attract other birds visually or through their vocalizations, resulting in increased foraging efficiency through the communal discovery of new food patches and enhanced predator avoidance (Barbosa 1995, Lima 1995, Battley et al. 2003). Finally, I modeled between-treatment distance because it might constrain movement,

and thus residency rates, if on average slow- and fast-managed wetland units were beyond the average movement range of birds. Although wetlands in YWC were functionally connected at distances of ≤ 2.5 km (Chapter 1) and average between-treatment distances were shorter, I felt that it was important to model its possible role in the context of management experiments.

Study Area

The Tom Yawkey Wildlife Center (YWC) is located in the Santee Delta-Cape Romain area of Georgetown County, South Carolina. It is a site of regional importance in the Western Hemisphere Shorebird Reserve Network. It harbors 5% of the flyway population or 20,000 individuals during the migratory season, including the Semipalmated Sandpiper (Marsh and Wilkinson 1991, Weber and Haig 1996). YWC is composed of approximately 8,000 hectares of marsh, maritime forest, upland pine forest, and ocean beach. YWC's three main islands (North Island, South Island and portions of Cat Island) are separated from the mainland by the Intracoastal Waterway.

The study area was located on South Island (79°15'W, 33°10'N). Management experiments were conducted in 13 brackish managed wetlands ranging in size from 12 to 69 ha. Each managed wetland unit has one primary, and in some cases, multiple secondary water control structures which allow managers to control the depth and drawdown rate of the managed wetland unit. Managed wetland units were characterized by gradually sloping bottoms of soft mud, surrounded by a perimeter ditch. While the majority of each managed wetland unit was open water, most have areas of widgeongrass (*Ruppia maritime*), sea purslane (*Sesuvium maritimum*), muskgrass (*Chara* spp.), saltmarsh bulrush (*Scirpus*

robustus), black needle rush (*Juncus roemerianus*), smooth cordgrass (*Spartina alterniflora*), and giant cordgrass (*Spartina cynosuroides*) (Weber and Haig 1996).

Managed wetland units were arranged in three sets of spatially segregated clusters. Every cluster contained at least a pair of managed wetland units under a slow and fast drawdown hydrologic treatment. Treatment allocation to individual managed wetland units depended on management objectives for vegetation control, the draining capability of the managed wetland unit, and study design considerations (e.g., pair up treatments per cluster). Treatment assignment per year and size (ha) of each managed wetland unit is listed in Table 1, and Figures 1a and 1b show the locations of the units within YWC. Within each cluster, units under study comprised the dominant or co-dominant feature in terms of suitable habitat for shorebirds. In clusters 1, 2, and 3, the proportion of wetlands managed for shorebirds was 69%, 54%, and 45%, respectively. The remaining wetlands in the clusters were unsuitable for shorebirds they were either flooded or completely drawn down and hardened.

For both years, a slow drawdown was implemented beginning in early spring (late March-early April) prior to the arrival of Semipalmated Sandpipers. The intended effect was to gradually make suitable habitat available to shorebirds beginning no later than mid-April; the onset of the migration season for Semipalmated Sandpipers in the YWC. In a fast drawdown, water levels were dropped in a matter of 2-3 days. The fast drawdown was implemented just prior to May 20th, or peak migration at the YWC (Marsh and Wilkinson 1991, Lyons and Haig 1995, Weber and Haig 1996).

Methods

Bathymetric Profiles

Bathymetry maps were constructed for each wetland unit in 2006 because changes in vegetation cover had occurred since 1999 (date of the most recent available aerial imagery) and no prior bathymetric profiles of the wetland units had been created. Bathymetry data were used to estimate accessible habitat (0-4 cm water depth) for shorebirds as a function of gauge readings every week in 2006, and daily in 2007, during the migratory season. I initiated the process by recording depth and a GPS reading every 9-10 m along 2-4 transects that bisected each management unit (see Chapter 1, Figure 2). Transects were positioned to account for as much heterogeneity in each unit as possible. Each unit was subsequently photographed from the air (~700 m) using an unmanned aerial vehicle (UAV). The UAV was operated by a team from the University of Florida Cooperative Research Unit. Aerial photographs were then digitized and geo-referenced to digital ortho quarter quads (DOQQs) of Yawkey Wildlife Center from 1999. Bathymetry data were then combined with the geo-referenced photos to produce maps depicting accessible habitat as a function of gauge readings.

Invertebrate Sampling

I sampled invertebrates three times in 2006 and 2007 to obtain estimates of prey biomass in each experimental managed wetland unit. In 2006, the initial sampling was conducted on 28-30 April, and then on 16-17 May (prior to peak of migration) and 1-4 June. Adjustments were made in 2007 to better match the implementation of the fast drawdown and shorebird migration. The initial sampling was conducted on 17-18 May. Subsequent

sampling events were a week apart (24-25 May; 31 May – 1 June). Invertebrates were collected from 13 primary sampling plots, one in each of the experimental wetland units. Plots were aligned with the bottom contour of the managed wetland unit to insure that “newly available habitat” would be sampled throughout the season. Each primary plot was 50 m x 5 m, subdivided into five secondary plots which were 10 m x 5 m. Within each secondary plot there were 50 subplots of 1 m². Within each primary plot, two 1 m² subplot sampling units were selected randomly during each sampling period and sampling was done “without replacement” because the subplots were altered during sampling (e.g., core sampling). A five gallon bucket (radius = 13 cm, height = 36 cm) with the bottom cut out was used to isolate the water column, preventing the escape of any aquatic invertebrates. The bucket was pushed through the water and into the bottom substrate in a random location within the randomly chosen subplot. I pumped the water into gallon zip lock bags for transport back to the field house. Once the water was extracted from within the bucket, I used a hand bulb planter (radius = 3.75 cm, height = 10 cm) to extract two mud core samples from within the area contained by the bucket. Each core sample of mud was 5 cm deep. The benthic core samples were placed in zip lock bags for transport to the field house. At the field house, 20 cm diameter sieves down to 425 microns (W.S. Tyler Company, Mentor, OH) were used to separate the invertebrates from the water or mud substrate. The water and benthic invertebrates were kept separate and placed in vials according the sample location and period, and preserved in a 10% formalin solution.

After the field season, the invertebrates were identified to either Class (Gastropoda, Polychaeta, Oligochaeta), Order (Amphipoda, Coleoptera, Diptera, Odonata, Trichoptera) or Family (Chironomidae, Corixidae) using a 20x dissecting microscope at North Carolina State

University. Invertebrates were placed individually or in groupings of five on Millipore glass fiber prefilters, and then placed in a Precision Gravity Convection Oven for four hours at 70° C in order to remove any water. Dried invertebrates were weighed using a Thermo Electronic Microbalance to the nearest 0.1 mg. Dried weights for the invertebrates were expressed as a density in milligrams per cubic centimeters of either water or mud for each sample.

Mark-Encounter Histories

In 2006, 500 birds were captured with mist-nets and individually color-marked during 10 banding sessions (1-3 days each) from 10 May – 28 May. In 2007, 502 birds were captured and marked over 16 banding sessions conducted every other day from 7 – 18 May and every day from 18 – 28 May. Captured birds were kept in a ventilated cardboard box up to 2 hours or until all birds were processed. Birds were weighed to the nearest 0.5 g using a Pesola spring scale and measurements of their flattened wing chord (carpal joint to the wing tip to the nearest 1.0 mm) and bill length (bill tip to feather margin on forehead to nearest 0.5mm) were also recorded. Colored bands were placed on the tibiotarsus. Birds were also outfitted with a metal USFWS band on their lower left leg (tarsometatarsus). This work was conducted under IACUC (Institutional Animal Care and Use Committee) permit number: 06-039-O.

In 2006, data consisted of only encounters of color-marked shorebirds. Encounter history data were generated by recording unique color combinations of 4 Darvic UV resistant UPVC colored leg bands assigned to each captured bird (2 on right leg, 2 on left leg). In 2007, I supplemented color-marking with radio telemetry to increase the probability of

detection, and thus, increase the likelihood of relating factors of interest in this study to shorebird responses. Low vegetation obstructed leg bands in some cases and some birds might have been missed if they occurred in the interior sections of the larger wetland units. Accordingly, 72 of the 502 Semipalmated Sandpipers captured in 2007 were also instrumented with transmitters. The 0.56 g radio transmitters (Model BD-2N Holohil Systems Ltd., Woodlawn, Ontario, Canada) were glued to the lower backs of each bird following methods described in Warnock and Warnock (1993). The radio transmitter was glued with waterproof epoxy (Liquid Bonding Cement, Torbot Group, Inc., Cranston, Rhode Island) to clipped feathers on the lower back about 5 mm anterior to the uropygial gland. The transmitters were less than the suggested 3% of a bird's body mass, and the retention time was expected to be less than 7 weeks (Bishop et al. 2004). Transmitters were allocated among the three clusters of wetland units on a rotating 3 day schedule banding every day from 18 May to 28 May and split near evenly between slow (37 birds total) and fast treatments (35 birds total). I placed transmitters on 18 birds (slow $n = 11$, fast $n = 7$) in cluster 1, on 10 birds (slow $n = 5$, fast $n = 5$) in cluster 2, and on 44 birds (slow $n = 21$, fast $n = 23$) in cluster 3. Transmitters were allocated among clusters based on their relative acreage and Semipalmated Sandpiper population size (e.g., cluster 3 had the largest area and thus the largest population of Semipalmated Sandpipers, while cluster 1 had the smallest area but the second largest observed population of Semipalmated Sandpipers).

Visual encounters (resights) in 2006 were obtained by surveying the study area every day (including banding day), except on three occasions when it was done at 2 day intervals to allow time for invertebrate sampling and shorebird surveys. Similarly, resight surveys in 2007 were performed every day (including banding days) except during invertebrate

sampling days. Tracking of instrumented birds was done every day of the season. During resight surveys, all managed wetland units under treatment (approximately 425 ha) were searched from the dyke surrounding each unit, as well as by walking into the units where substrate and water depths allowed. Telemetry searches were performed using R-1000 telemetry receivers (Communication Specialists, Inc., Orange, CA) with an RA-14K “H” style handheld antenna (Telonics, Inc., Mesa, AZ). Tracking was done in teams of two to simultaneously locate telemetered birds using triangulation from 14 pre-determined listening stations placed throughout the study area.

Bird Population Index

Weekly shorebird counts were conducted to obtain an idea of changing population numbers at YWC. However, because I could not sample each of the managed wetland units in their entirety, I made counts from three randomly located survey points at each managed wetland unit and treated it as an index of the population size. Counts at each managed wetland unit were made within a 100 m radius fixed area of the point to standardize results (birds/unit area). Within the 100 m area, I assumed that detection was 1 or nearly so.

Wind

The possible influence of “southerly winds” on shorebird residency was modeled using an expression that excluded all winds that could be considered “head winds” or those less than 90 degrees or greater than 270 degrees. Winds from a southerly direction might aid northbound shorebirds in their movement among stopover areas (Butler et al. 1997). This covariate was calculated as $swind = -\sum v_i \cos\theta_i I_i$, where $I_i = 1$ if $\cos\theta_i$ is < 0 , otherwise $I_i = 0$

(J. E. Lyons, Patuxent Wildl. Res. Ctr, pers. comm.). The closest source of wind data to YWC was the Charleston International Airport, 80 km south of YWC. Hourly surface wind data were collected by the National Climatic Data Center. Surface winds were used because they are the cues birds on the ground use to identify winds aloft (Skagen and Knopf 1994b, Åkesson and Hedenström 2000, Liechti 2006).

Data Analysis

Shorebird count data (birds/ha) were analyzed using ANOVA with survey period, treatment, and the interaction survey*treatment as model terms (JMP 1994). The response variable was log-transformed to meet homogeneity of variances assumption. Similarly, invertebrate data were analyzed using ANOVA with the response variables being the biomass of invertebrates (all taxa, all substrates). Model terms were sampling period, treatment, managed wetland unit within treatment and interaction between period and treatment (JMP 1994). Invertebrate data were power-transformed to meet homogeneity of variances assumption.

I combined invertebrate taxa by substrate because most taxa were detected (90%) in all sampled units and because prey biomass for most taxa did not differ between treatments (Appendix I). Semipalmated Sandpipers are known to prey on all of the prey items found in YWC (Weber and Haig 1996), and like most migratory shorebirds, they are known for their dietary flexibility (Skagen and Oman 1996, Parrish 2000). Therefore, it is unlikely that pooling data by substrate masked the influence of any particular prey item on foraging patterns by migrant Semipalmated Sandpipers in response to drawdown schedules. This

possibility was further minimized by re-assigning treatments to most managed units between 2006 and 2007.

Weight and wing chord measurements were used to calculate estimated percent fat (epf), which is a body condition index, for each bird based on the equation $epf = 100 ((WT - FFW)/WT)$, where WT is the total body weight and FFW is the fat-free weight (Page and Middleton 1972, Dunn et al. 1988). Fat-free weights were calculated based on the equation $FFW = -9.0513 + 0.3134 (\text{wing length})$ (Page and Middleton 1972). Patterns of epf change over time per year were examined using ANOVA (JMP 1994). Model terms were time period, treatment and interaction. This analysis was restricted to 2007 when birds in both treatments were collected only 1 day apart. Such a contrast in 2006 would not be appropriate because (1) fewer samples were collected and (2) the time interval between them was 4 days. Epf is believed to increase with time at stopovers (e.g., Lyons and Collazo in press).

I expressed accessible habitat as the proportion within each treatment because, unlike 2006, the amount of hectares under each treatment in 2007 was markedly different. In 2006 there were a total of 179 ha under fast treatment and 195 ha under slow treatment, while in 2007 there were a total of 81 ha under fast treatment and 336 ha under slow treatment. The proportion of accessible habitat was calculated as:

$$\text{Proportion of accessible habitat} = \frac{\text{total area (ha) of accessible habitat in treatment of interest}}{\text{the total area (ha) of accessible habitat in both treatments}}$$

In 2006, I estimated residency (\hat{S}) and movement ($\hat{\psi}$) rates based on encounter histories from visual recaptures or resight data. In 2007, I combined encounter histories from resight (collected from 8 May to 11 June) and telemetry (collected from 18 May to 11 June) data. A joint analysis of the two data types, referred to as group (g) in models, has the

advantage of increased precision of estimates as well as the ability to test for differences in the encounter rates of the two cohorts (Nasution et al. 2001). In 2006, there were 22 sampling occasions, or 21 intervals. In 2007, there were 24 sampling occasions or 23 intervals. Every sampling occasion represents a complete search of the refuge. In most cases this search took 1 day, but in a few instances complete coverage took 2 days. I also estimated the mean length of stay (MLS) of shorebirds each year using: $MLS = -1/\ln(\text{daily residency probability})$ (Brownie et al. 1985). Estimates should be taken only as an approximation of MLS because this formula assumes constant survival and previous work modeling shorebird residency rates has shown that rates vary seasonally (Dinsmore and Collazo 2003, Lyons and Collazo 2005). Estimates reported herein are based on the seasonal average of daily residency probabilities.

Five covariates were used to model residency and movement rates in 2006. These were estimated percent fat (epf), speed of southerly winds (Swind), index of bird density (average birds/ha), and proportion of accessible habitat/treatment, total area (ha) under a specific treatment. In 2007, two additional covariates, prey density (mg/cm^3) and average distance between treatments (proximity) were modeled. Estimated percent fat and southerly winds were used only to model their influence on residency rates. Conversely, total area of wetland units under each treatment and average distance between treatments were used only to model their influence on movement rates. These covariates were modeled as additive effects on either constant or time-varying S and Psi models using reduced parameter models. Time-varying models also included linear (T) or quadratic (TT) terms as it has been shown the residency rates may vary in a curvilinear fashion (e.g., Dinsmore and Collazo 2003) and I hypothesized that movement rates might increase or decrease as a function of MLS.

Values of area and proximity were constant, and epf was measured at capture for every bird. Wind and accessible habitat data in 2007 were collected on every sampling occasion and manually entered to model their effects on time-varying S and Ψ using reduced parameter models. In 2006, accessible habitat data were collected weekly. Bird density index and prey biomass data were collected on fewer occasions due to field logistic constraints. Bird density index was estimated weekly on five occasions; prey biomass was estimated on three occasions. Although I acknowledge that this was a limitation, my goal was primarily to gain insights about the influence of these variables on a time varying context with as many estimates as logistics permitted. To minimize spurious interpretation of results, data were collected in the shortest possible intervals and were closely aligned with migration events and treatment implementation. For this reason, I chose to model only prey data from 2007. Prey was first sampled on 17-18 May 2007, closely matching peak shorebird migration and implementation of the fast drawdown. Subsequent sampling events were on 24-25 May and 31 May – 1 June, a week apart. Moreover, when prey biomass was modeled for 2006, values of beta coefficients were unusually high suggesting that predictions would be suspect (e.g., exponentiation problems).

I expressed accessible habitat (ha) in relative terms (i.e., proportion in treatment of interest/sum of accessible habitat in both treatments) to account for the different areal extent under each treatment type. Distance between a selected treatment and the nearest next treatment (proximity) was expressed as the average distance from the perimeter of each managed wetland unit under one treatment (i.e., slow) to the closest point on the perimeter of every managed wetland unit under the other treatment (i.e., fast). Distances were obtained using ArcGIS. The estimate of proximity in 2006 was equal (984.25 m) or approximately ~1 km, and thus, this covariate was not modeled. Proximity was modeled in 2007 because the assignment of

treatments among managed wetland units yielded different estimates. In 2007 the average distance between fast-managed units to the nearest slow-managed wetland units was ~1 km (1095.5 m), whereas it was ~1.5 km (1522.9 m) from slow- to fast-managed wetland units.

Finally, I modeled the interaction between epf and southerly winds. While epf is index of body condition measured at capture, 500 birds were captured throughout the season. The range of values collected over time provided an opportunity to explore if epf interacted with daily wind patterns. I also constructed models to explore the interaction between prey biomass and accessible habitat for 2007 models. The rationale for the interaction stemmed from the fact that prey for Semipalmated Sandpipers occurred in both the water column and muddy substrate. As such, patterns of prey richness and biomass may vary with water levels. It follows that foraging quality might be highest when physical conditions allow shorebirds to forage in both substrates simultaneously ($\leq 0\text{-}4$ cm water depth).

I constructed 33 and 58 models to evaluate variation in residency rates (S) and movement rates (ψ) in 2006 and 2007, respectively. The *a priori* model sets included pre-defined, naïve models as well as reduced parameter models (Appendices II and III). The 2007 models included encounter histories made up of visual (resight) and telemetry data. Recapture rates were modeled either by accounting encounter source (i.e., visual and telemetry) or combining encounters regardless of source. Naïve models accounting for encounter probability by source (i.e., $\{p(g)\}$) ranked higher than constant $\{p(.)\}$ or time-varying models $\{p(t)\}$. Thus, most models in the *a priori* model set were modeled with encounter probabilities by source (g), followed by constant encounter probability. Models with encounter probability by group over time (i.e., $\{p(g*t)\}$) were not considered because recapture probability was not estimable for many intervals.

Analyses were done using the “multi-strata recaptures only” module in Program MARK (White and Burnham 1999). I used the Akaike’s Information Criterion to select the most parsimonious model (Burnham and Anderson 2002). Models with $\Delta AICc \leq 2$ were considered models with highest support. I could not obtain an estimate \hat{c} to adjust models for overdispersion, much of it probably stemming from the gregarious behavior of shorebirds. The 2006 models had observed \hat{c} values ranging from 2.29 to 2.63, which suggested model selection was not unduly affected because values were ≤ 3.0 (Lebreton et al. 1992, pp. 84-85). However, some 2007 models had observed \hat{c} values of 4.28 to 4.37. As suggested by Cooch and White (2006), I assessed the sensitivity of top models to increasing values of median \hat{c} (e.g., 1.5, 2.0, 2.5). This ad hoc process leads to more conservative model selection (i.e., fewer parameters) and can suggest if other models should have received greater support. Adjustments re-ordered top four models ($\Delta AICc \leq 2$), but re-ordered models did not contain new terms (covariates) influencing S or Ψ . Substantial re-ordering of models, coupled with relative low $AICc$ weights, suggested that there was substantial uncertainty with regards to model selection in 2006 and 2007 (see RESULTS). Therefore, I model-averaged over the top models to account for this uncertainty (Cooch and White 2006). Because the number of models explored was large, I only report those with a $\Delta AICc \leq 10$ (Burnham and Anderson 2002). Finally, I used estimates of \hat{S} and $\hat{\psi}$ to separate movement and residency probabilities by treatment (Cooch and White 2006). I was interested in depicting the probability of a shorebird surviving and not moving from a particular treatment (i.e., $\hat{\Phi}^{SS}$ or $\hat{\Phi}^{FF}$). Expressing results in this fashion should aid readers to discern better the possible functional value of drawdown treatments to shorebirds.

Careful consideration of four model assumptions is important to interpret these results. First, I assumed that every color-marked bird had the same probability of being resighted in sampling period i and that every marked bird had the same probability of surviving from sampling period i to $i+1$, assuming that it was alive and present in the population at the time the survey was conducted. The same applied to instrumented birds. Second, I assumed that emigration (i.e., departure) was permanent. I believe that this assumption was met because coverage of the study areas was frequent and surveys included all available shorebird habitat at YWC, reducing chances that color bands or instrumented birds were overlooked (e.g., temporary emigration). Support for my assumption also comes from the work of Lyons and Collazo (2005). They found no evidence of temporary emigration problems during their study of telemetered Semipalmated Sandpiper at YWC in 2001 after routinely checking adjacent wetlands during aerial surveys. Some birds might have emigrated to near-by sandbars and mudflats adjacent to South Island in Winyah Bay and along the ocean beach (Weber and Haig 1996), but these areas are used for roosting. Foraging takes place within YWC. Third, I assumed that marks (i.e., color bands, transmitters) were not lost and that in the case of color bands, all were correctly recorded. This assumption was corroborated at least for transmitters—no losses were recorded during this study. Parameter estimates were reported as estimate \pm standard error.

Results

Bird counts fluctuated seasonally, peaking around the second and third week of May (Figure 2). Average bird density differed significantly by treatment in 2006 (slow $\bar{x} = 1.02$, fast $\bar{x} = 0.40$; $F = 5.57$, $df = 1, 43$, $p = 0.02$, Figure 3a). Bird density varied by survey

occasion (time) and treatment ($F = 2.74$, $df = 9, 35$, $p = <0.001$). Patterns of bird density did not differ significantly between treatments or over time in 2007 ($F = 0.009$, $df = 1, 43$, $p = 0.93$, Figure 3b).

The average epf value in 2006 was 13.56 (SE = 1.21) and 15.22 (SE = 1.69) in 2007. Epf values in 2007 were not significantly different between treatments ($F = 0.06$, $df = 1, 139$, $p = 0.81$). The average epf value in fast-managed wetland units was 15.373 (95% CIs = 13.265 - 17.481) whereas it was 14.938 (95% CIs = 12.050 - 17.827) in slow-managed wetland units (Figure 5).

The daily total area (ha) of accessible shorebird habitat (0-4cm) in managed wetland units increased with time as expected (Figures 5a, b). Depicting the percent of accessible habitat provided a clearer picture of the immediate response to the rapid drawdown (Figures 6a, b). Also as expected, rainfall events (e.g., 2 June 2007) reversed temporarily the increasing trends in accessible habitat.

Prey biomass in 2006 varied significantly by sampling occasion and treatment ($F = 3.97$, $df = 2, 14$, $p = 0.04$). Prey biomass in fast-managed units was lower than in slow-managed units (Figure 7a). There was also evidence that prey biomass varied by impoundment within treatment ($F = 3.85$, $df = 7, 14$, $p = 0.02$). In 2007, prey biomass was significantly lower in fast-managed units ($F = 15.04$, $df = 1, 20$, $p = 0.0009$). Average prey biomass in fast-managed wetland units was 0.09 mg/cm^3 , where as it was 0.21 mg/cm^3 in slow-managed wetland units (Figure 7b). There was evidence that prey biomass varied among managed wetland units within treatments ($F = 2.52$, $df = 10, 20$, $p = 0.04$), reflecting the heterogeneity of prey availability regardless of management.

In 2006, residency rates were best described by a model with a curvilinear trend in daily survival rates (TT), epf, southerly wind (Swind) and an interaction between epf and Swind (AICc weight = 0.22, Table 2). Model-averaged trends in residency rates were similar for birds marked in either treatment (Figure 8). The mean length of stay for birds marked in fast-managed units was 2.63 days (95% CIs = 2.23 - 3.03) and for birds marked in slow-managed units was 3.10 days (95% CIs = 2.53 – 3.68). Resight probability for this model was constant (0.082; 95% C.I. = 0.063 - 0.106). The interaction between epf and Swind was significant and negative ($\hat{\beta} = -0.018$; 95% CIs = -0.0329 to -0.0026; Table 3). Variation in movement probability was best explained by a curvilinear trend (TT) and the proportion of accessible habitat by treatment. Accessible habitat significantly and negatively influenced movements rate ($\hat{\beta} = -2.447$, 95% C.I. = -4.830 to -0.064). Model-averaged movement rates increased seasonally and differed significantly (non-overlapping CIs) during occasions 4-11 (Figure 9). Average movement rates from fast- to slow-managed wetland units was 0.399 (95% C.I. = 0.185 - 0.614). Conversely, average rates from slow- to fast-managed wetland units was 0.227 (95% C.I. = 0.110 - 0.346). Patterns of Phi ($\hat{\Phi}$) suggested that residency of birds marked in either treatment was greater at slow-managed units (Figure 10). It was noteworthy that the poorest use of fast-managed wetland units occurred soon after full the implementation of the rapid drawdown (occasion 6).

Based on $\Delta AIC (\leq 2.0)$, there were four other competing models (Table 2). The second best model featured bird density as a factor positively and significantly influencing variation in movement rates. The third best model incorporated bird density as influencing residency rates and proportion of accessible habitat as significantly and negatively

influencing movement rates. The fourth top model had residency and movement rates influenced by bird density, and the fifth top model differed in that the proportion of accessible habitat influenced both residency and movement rates.

In 2007, residency rates were best explained by a model with a quadratic term (TT), bird density, epf, southerly winds (Swind), and an interaction between epf and Swind (AICc weight = 0.24, Table 4). The epf*Swind interaction was significant and negative ($\hat{\beta} = -0.011$, 95% CI = -0.019 to -0.003; Table 5). Bird density positively and significantly influenced residency rates ($\hat{\beta} = 0.678$, 95% CI = 0.080 – 1.276). The mean length of stay for birds marked in slow-managed units was 5.369 days (95% CI = 2.863 – 7.875) and 5.74 days (95% CI = 3.733 – 7.750) in fast-managed units. Resight probability for color-marked birds was 0.11 (95% CI = 0.091 - 0.138) and for telemetered birds was 0.70 (95% CI = 0.641 - 0.753). Movement rates were negatively but not significantly influenced by prey biomass ($\hat{\beta} = -1.886$, 95% CI = -4.464 – 0.692). Based on $\Delta AIC (\leq 2.0)$, there were three other competing models (Table 4). All alternative models featured the negative influence of prey biomass on movement rates. Bird density appeared along with prey biomass in only one model. The positive influence of prey biomass and bird density or prey biomass and access were featured along with epf and Swind as factors influencing residency rates in alternative models (Table 4).

Model-averaged trends indicated that birds in fast-managed units had higher residency rates (\hat{S}) than in slow-managed units while at YWC, significantly so during occasions 9-15 (Figure 11). The probability of moving from fast- to slow-managed wetland units was high early in the season, followed by a marked drop after the rapid drawdown was

implemented (occasion 7, Figure 12). Rates were significantly different throughout the season (i.e., non-overlapping CIs). The average movement rate of fast- to slow- managed wetland units was 0.467 (95% CIs = 0.406 – 0.527) where as movement rates in the opposite direction averaged 0.055 (95% CIs = 0.044 – 0.066). The probability of surviving and not moving for birds in slow-managed units ($\hat{\Phi}^{SS}$) post-treatment averaged 0.654 (95% CIs = 0.595, 0.713) (Figure 13). Conversely, the probability of birds surviving and not moving from fast-managed units ($\hat{\Phi}^{FF}$) averaged 0.399 (95% CIs = 0.353, 0.445) after the full implementation of the draw down. Daily estimates of $\hat{\Phi}^{FF}$ never exceeded $\hat{\Phi}^{SS}$.

Discussion

Models with highest support, regardless of year, highlighted the influence that estimated percent fat and southerly winds exerted over residency rates. The significant and negative interaction between these factors meant that differences in departure rates between birds of varying body condition were minimized. In other words, it was possible for birds of high and low epf values to depart YWC on the same occasion as had been reported for Semipalmated Sandpipers in mid-continent stopover sites (Skagen and Knopf 1994). A factor facilitating this possibility was the strength and frequency of southern winds (Chapter 1, Weber et al. 1998, Åkesson and Hedenström 2000). These factors were also featured in models exploring residency and movement rates among clusters of wetlands at YWC and residency rates at the refuge level (Chapter 1). The consistent presence of these factors in analyses at various scales attests to how local and larger-scale factors interact to mold migration strategies (Skagen and Knopf 1994, Lyons and Haig 1995, Farmer and Weins 1999, Sanzenbacher and Haig 2002).

In this hierarchical framework, I hypothesized that shorebirds would remain at or move to and remain at newly created habitat while at YWC. A determinant factor influencing these patterns would be higher levels of prey biomass made available after a rapid draw down. Support for my hypothesis was weak. Evidence collected over two field seasons indicated that shorebirds responded to the sudden availability of accessible habitat as expected. However, the rate at which birds moved towards fast-managed wetland units was significantly lower in 2006 and 2007 than movement in the opposite direction. By and large, birds marked in slow-managed wetland units tended to remain there. Conversely, birds marked in fast-managed wetland units had lower to significantly lower chances of remaining in those units.

In 2006, the probability of surviving and not moving in fast-managed wetland units ($\hat{\Phi}^{FF}$) increased as the season progressed, but did not exceed $\hat{\Phi}^{SS}$ post-treatment. A plausible explanation for these patterns is that management created accessible, functionally connected habitat but of dissimilar value. Slow-managed wetland units had higher prey biomass, significantly so at the time when the full effects of the fast draw down were recorded (occasion 6). Thus, while birds were able to move between units under both treatments, slow-managed units continued to receive higher use. Connectivity is relevant in this discussion because models suggested that inter-treatment distance was not a constraint on inter-treatment movement patterns. Birds moved 1.6 km, on average (Chapter 1), which was greater than the inter-treatment distance in 2006 and 2007. Encounter history data were not sufficient to jointly model the influence of inter-cluster and between-treatment distances (3 clusters * 2 treatments). However, I do not believe that my inferences about between-treatment movements are unduly biased because treatments occurred within clusters that

were functionally connected (≤ 2.5 km, Chapter 1). Finally, I speculate that bird density could have contributed to the higher residency of slow-managed units. Density of birds in slow-managed wetland units was significantly higher and its positive influence on residency rates was featured in 3/5 competitive models ($\Delta AICc \leq 2.0$). Bird aggregations tend to draw other birds and enhances opportunities for locating new food patches while minimizing the risk of predation (Barbosa 1995, Lima 1995, Battley et al. 2003).

Inferences from 2006 were strengthened by patterns of residency and movement rates in 2007. Birds tended to significantly remain in slow-managed wetland units (avg $\hat{\Phi}^{SS} = 0.654$). Birds also exhibited a significantly higher probability of moving out of fast-managed wetland units (avg $\Psi = 0.554$) and significantly lower probability of remaining in those units (avg $\hat{\Phi}^{FF} = 0.399$). Differences in residency were greater likely because prey biomass was significantly higher in slow-managed units throughout the season, unlike 2006 when significance was detected only during the middle of the season. The prevalence of prey biomass in all top, competitive models attested to its importance in influencing both residency rates (positive) and movement rates (negative). Shorebirds are selectively attracted to areas with higher food abundance (Hicklin and Smith 1984, Colwell and Landrum 1993, Farmer and Parent 1997, Placyk and Harrington 2004, Taft and Haig 2006), selecting among available habitats in relation to long-term net energy gains (Laubhan and Gammonley 2000). The proclivity of birds to move out of the fast-managed wetland units suggested that birds had to invest more time searching for suitable habitat, perhaps contributing to the higher residency (\hat{S}) at YWC immediately after the implementation of the rapid drawdown. Admittedly, the negligible movement rates away from slow-managed wetland units might

have been influenced by the higher number of hectares (336) under a slow treatment as compared to units under a fast treatment (81 ha). This disparity was modeled by expressing accessible habitat in relative terms in time-varying models and as an additive effect in constant Psi models. The latter models did not receive support ($\geq 10 \Delta AICc$; Burnham and Anderson 2002) and the former suggested that accessible habitat had a negative, albeit not significant, influence over residency rates. Thus, I still believe that ultimately prey, not accessible habitat, influenced residency for the reasons articulated above.

One of the aims of a fast drawdown is to provide diverse and high quality habitat quickly during peak migration. It calls for maximizing the extent of habitat available to the bulk of the population during a period of high maintenance and energetic requirements (Myers et al. 1987). However, my findings suggested that the presumed advantage to birds was predicated on several high-risk suppositions. First, prey biomass could be markedly lower in fast-managed wetland units, as documented in this study. This possibility undercuts the very premise behind the implementation of fast drawdowns. Birds will respond to the physical stimulus created by the rapid draw down, but by the same token, birds will move out if differential prey conditions are encountered. Use of fast-managed wetland units might also be dampened if newly created habitat represents a low proportion of suitable habitat in the conservation area. Under such circumstances, extent, connectivity and quality of the competing treatment (i.e., slow drawdown) might lead to low use of fast-managed wetland units (Φ^{FF}) even if prey biomass are similar between treatments (Belisle 2005). My work also suggested that use of habitat created by fast drawdowns might be dampened by the presence and activity of foraging flocks on neighboring slow-managed wetland units (Barbosa 1995, Lima 1995, Battley et al. 2003; Chapter 1). Flocking also helps shorebirds to

offset the costs of predation (Cresswell 1994, Barbosa 1995, Ydenberg et al. 2002, Pomeroy 2006). This benefit is more likely accrued in sites shared with other shorebirds.

Another risk associated with the implementation of rapid drawdown is missing the intended target of peak migration. Brief layovers and annual variation on migration schedules conspire to increase that possibility, as illustrated by this work. In both 2006 and 2007, peak migration occurred around May 14-16, or 5 days before the full effects of a fast drawdown. Previous research suggested that peak migration occurred around May 20th at YWC (e.g., Marsh and Wilkinson 1991, Lyons and Haig 1995, Weber and Haig 1996). Finally, the challenges of timing the drawdown precisely could be compounded by operational considerations (J. Dozier, Manager, YWC, pers. comm.). Flooded wetland units might not allow managers to determine if a water control structure is functional. Potential problems will become apparent only after the attempt to dewater the unit rapidly is implemented. The time required to fix such units usually extends past the migratory season (J. Dozier, YWC, pers. comm.).

My findings suggested that unless local conditions preclude alternatives, fast drawdowns should not constitute the primary management scheme to meet habitat requirements for migratory shorebirds, at least in the southeastern United States. As suggested by many before me, habitat objectives can be adequately met by implementing a series of staggered, slow drawdowns (see Rundle and Fredrickson 1981, Breininger and Smith 1990, Colwell and Taft 2000, Isola et al. 2000, Collazo et al. 2002, Parsons 2002, Taft et al. 2002). My study strengthened the rationale justifying the implementation of this scheme by quantifying functional responses of shorebirds in the context of management experiments.

Effective design and implementation of staggered, slow drawdowns relies on basic knowledge about prey base dynamics, hydrologic capabilities at hand to attain specified water depth levels, and knowledge about timing, duration and average size of shorebird populations at a stopover (Loesch et al. 1995, Weber and Haig 1996, Collazo et al. 2002). This study also stressed the importance of functionally connected management units (see also Chapter 1). The following recommendations should be followed to enhance habitat for migrant shorebirds:

1. Establish a relationship between water gauge readings and the amount of accessible habitat for each management unit of interest. This can be accomplished by conducting bathymetric surveys as those described in this work or by Collazo et al. (2002) and Taft et al. (2002).
2. Staggered, slow drawdowns should be implemented throughout the season to provide habitat for early migrants, but maximize the amount of accessible habitat for peak migration. Implementation should strive for depths ranging from 0-8 cm to accommodate a wide array of species (Weber and Haig 1996, Davis and Smith 1998, Collazo et al. 2002). Estimates of the number of hectares required throughout the season can be obtained following recommendations outlined by Loesch et al. (1995). If site-specific estimates of mean length of stay are not available, Lyons and Collazo (2005) recommend using 10 days for the southeastern United States.

3. Understanding prey dynamics is essential to make sure that high quality habitat is made available to shorebirds (Weber and Haig 1997, Collazo et al. 2002). Periodic prey sampling is recommended to ensure that estimates of required habitat reflect actual prey levels.

4. Multiple management units should be functionally connected, particularly if they occur within a single conservation area. The ease of movement to and from different managed wetland units enhances foraging success while reducing the costs of searching for high quality sites (Farmer and Parent 1997, Goodwin 2003). At the Yawkey Wildlife Center clusters of wetlands were functionally connected at distances of ≤ 2.5 km. Within a cluster, average distances among managed units were considerably lower and were not found to be an impediment to shorebird movements. The 2.5 km distance reported in this study was slightly greater than 1.1 km reported for Pectoral Sandpipers in ephemeral wetlands in the mid-continent (Farmer and Parent 1997) and similar to the 2 km reported for over-wintering Dunlins in inland wetlands in Oregon (Taft and Haig 2006).

Table 1. List of treatment assignments to managed wetland units at the Tom Yawkey Wildlife Center, South Carolina in 2006 and 2007. Treatments were either a slow (S) or fast drawdown (F). The size (ha) of managed wetland units, the cluster where it belonged, and an identification number are also listed. The identification number corresponds to each unit's number in Figure 1.

Managed Wetland Unit	Unit Map Number	Size (ha)	Cluster	Treatment	
				2006	2007
Cooperfield	1	13	1	n/a	F
Blackout Pond	2	34	1	F	S
Penfold Pond	3	22	1	S	n/a
Southeast Goose Pasture	4	28	2	F	F
Southwest Goose Pasture	5	55	2	S	S
Northern Reserve	6	23	3	F	S
Lady's Pond	7	12	3	n/a	F
Upper Lower Reserve	8	27	3	S	S
Middle Lower Reserve	9	69	3	S	S
Lower Lower Reserve	10	18	3	n/a	S
Twin Sisters Pond	11	65	3	F	S
Santee Pond	12	45	3	S	S
Upper Pine Ridge Pond	13	28	3	F	F

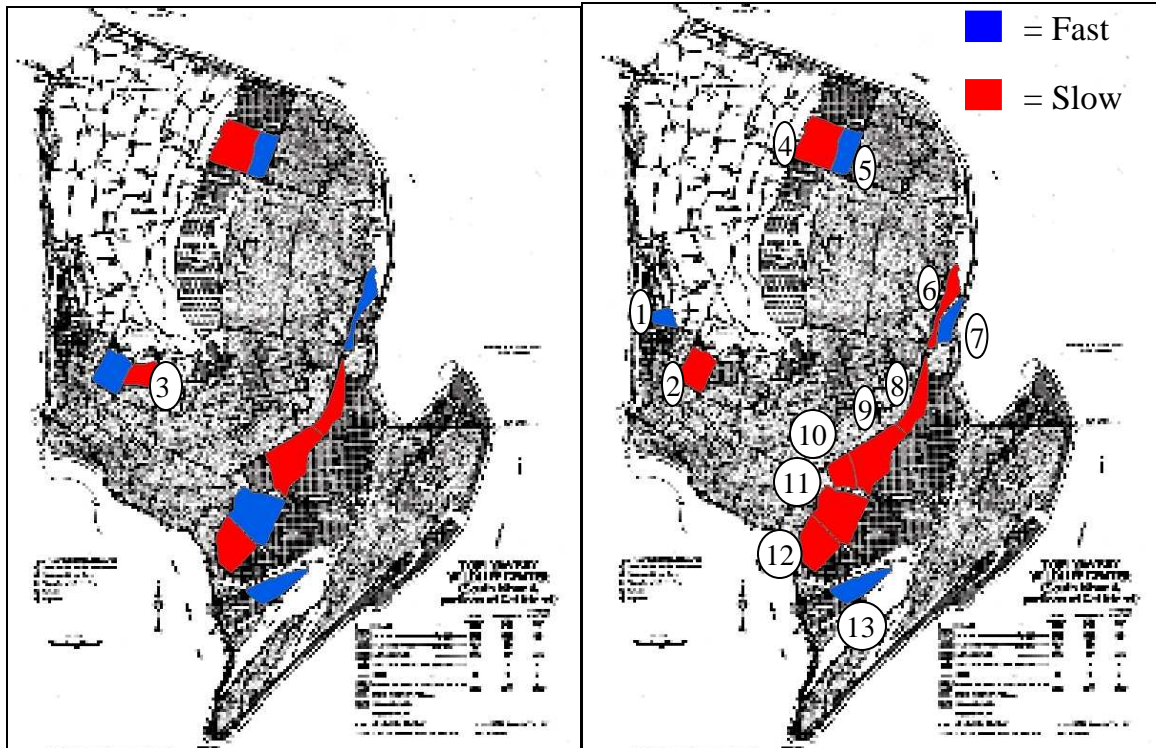


Figure 1. Map of the Tom Yawkey Wildlife Center, South Carolina showing the location of managed wetland units under experimental manipulation to estimate residency and movement rates of Semipalmated Sandpipers during Spring migration of 2006 and 2007. Wetland units were either under a slow (S) or fast (F) draw down regime. Left panel (1a) is the treatment allocation in 2006; right panel (1b) is the treatment allocation in 2007. Managed wetlands were numbered to correspond to Table 1.

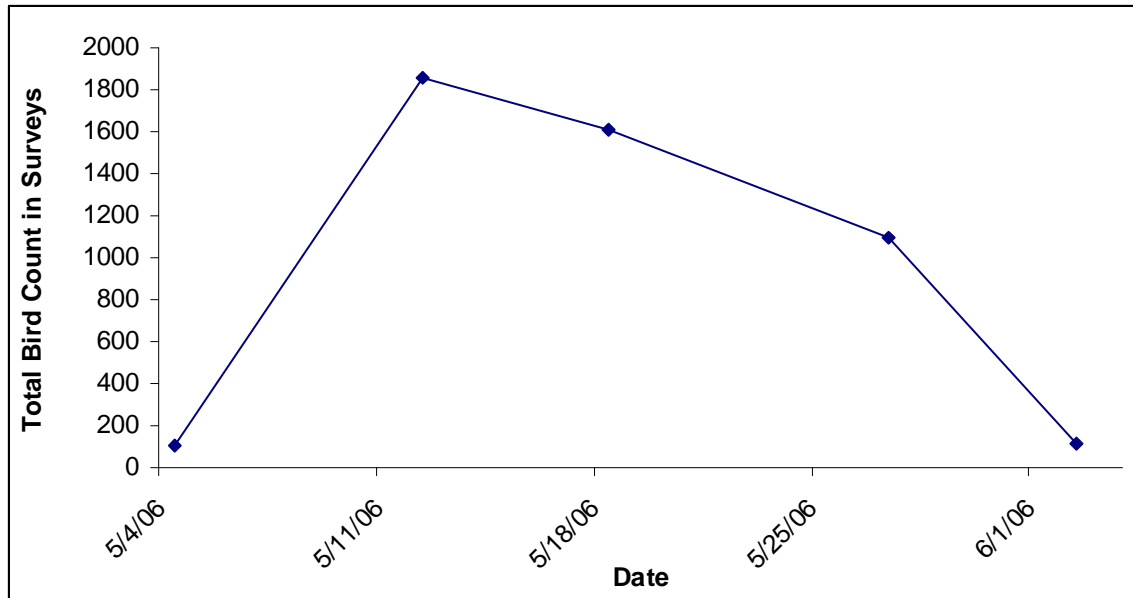


Figure 2. Total number of Semipalmated Sandpipers counted at 33 survey points (3 in each of 11 managed wetland units) at the Tom Yawkey Wildlife Center, South Carolina during Spring migration 2006. Surveys were conducted on May 4th, May 12th, May 18th, May 27th, and June 2nd. A total of 9.42 ha were surveyed in clusters 1 and 2 each period, and a total of 23.56 ha were surveyed in cluster 3 each period.

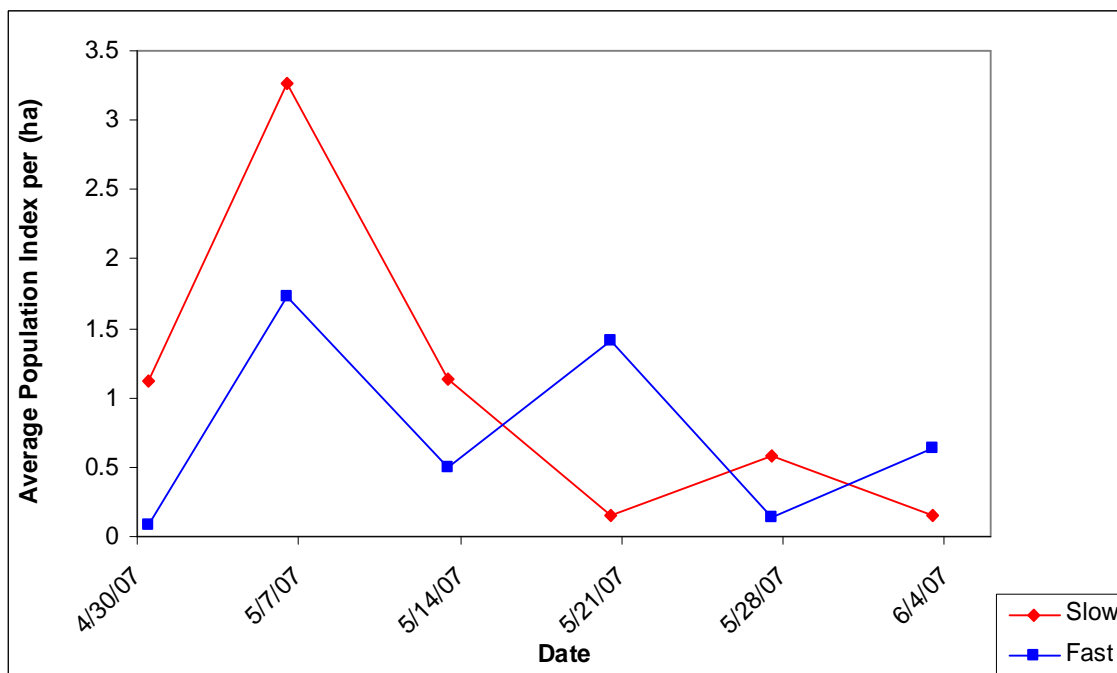
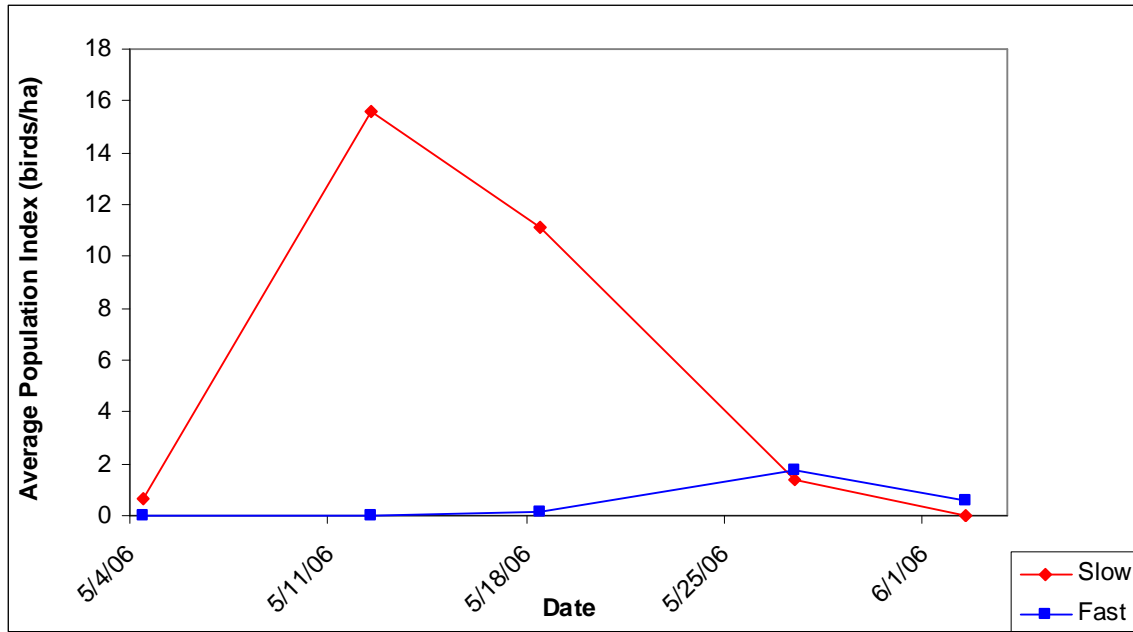


Figure 3. Average weekly estimate of Semipalmated Sandpipers per hectare (ha) in slow- and fast-managed wetland units at the Tom Yawkey Wildlife Refuge, South Carolina during Spring migration in 2006 and 2007. Top panel (3a) depicts pattern in 2007; bottom panel (3b) depicts pattern in 2006.

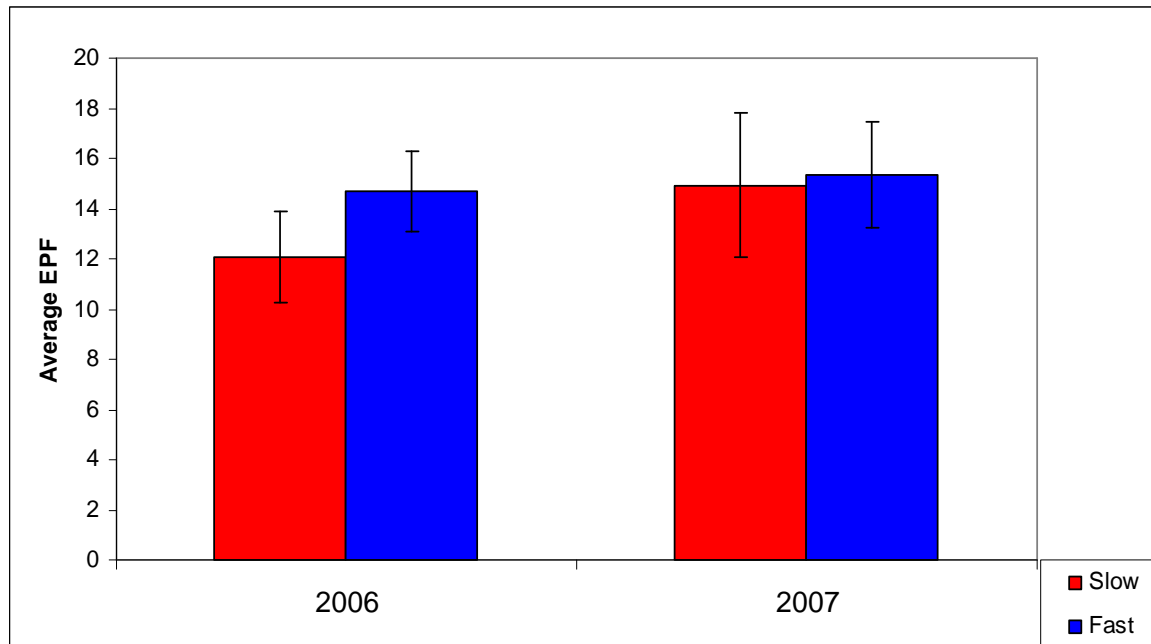


Figure 4. Average estimated percent fat (epf) at capture (\pm SE) for Semipalmated Sandpipers in fast- and slow-managed wetland units at the Tom Yawkey Wildlife Center, South Carolina. Data in 2006 were collected on 20-21 May in slow-managed units and on 26-28 May in fast-managed units. Data in 2007 were collected on 20, 24 and 26 May in slow-managed units and on 21, 23, 27 and 28 May in fast-managed units.

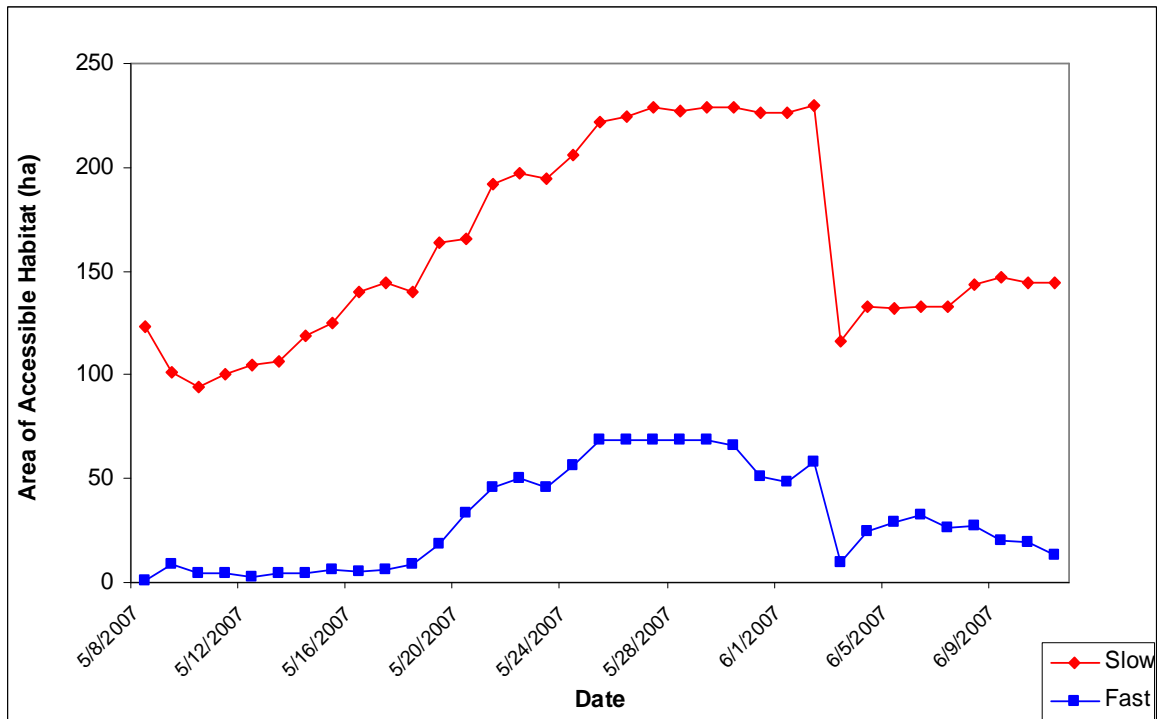
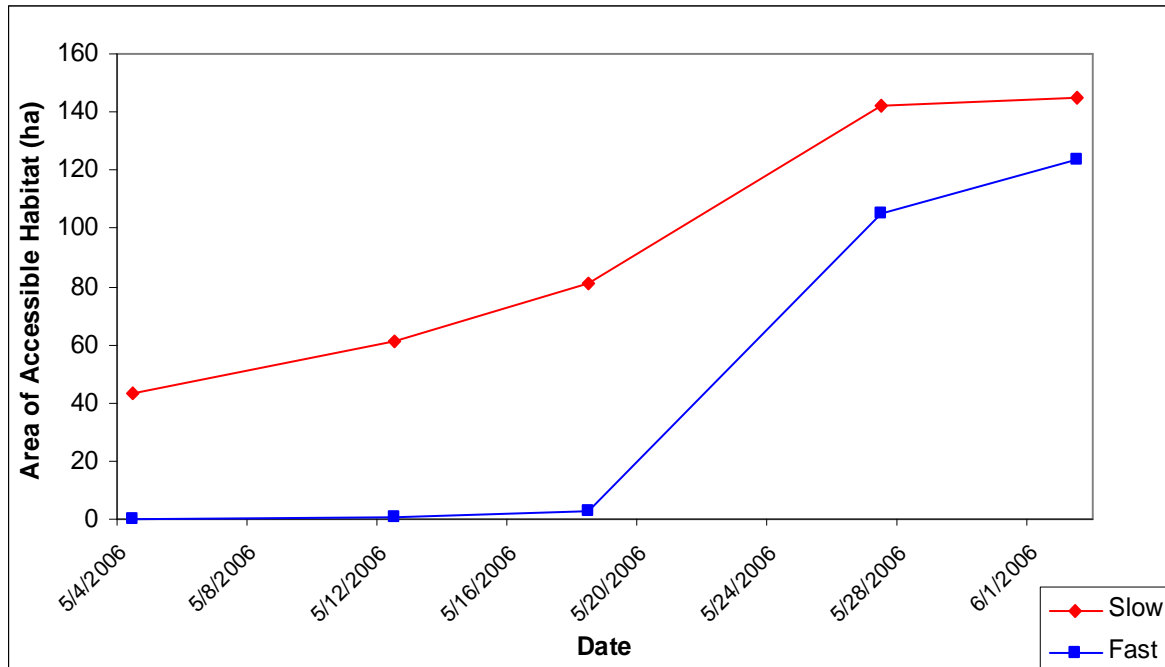


Figure 5. Number of hectares of accessible habitat (0-4 cm) made available to Semipalmated Sandpipers under a slow and fast draw down regime at the Tom Yawkey Wildlife Center, South Carolina. Top panel (5a) depicts seasonal pattern in 2006; bottom panel (5b) depict pattern in 2007. The fast draw down was implemented on 17 May 2006 and 17 May 2007.

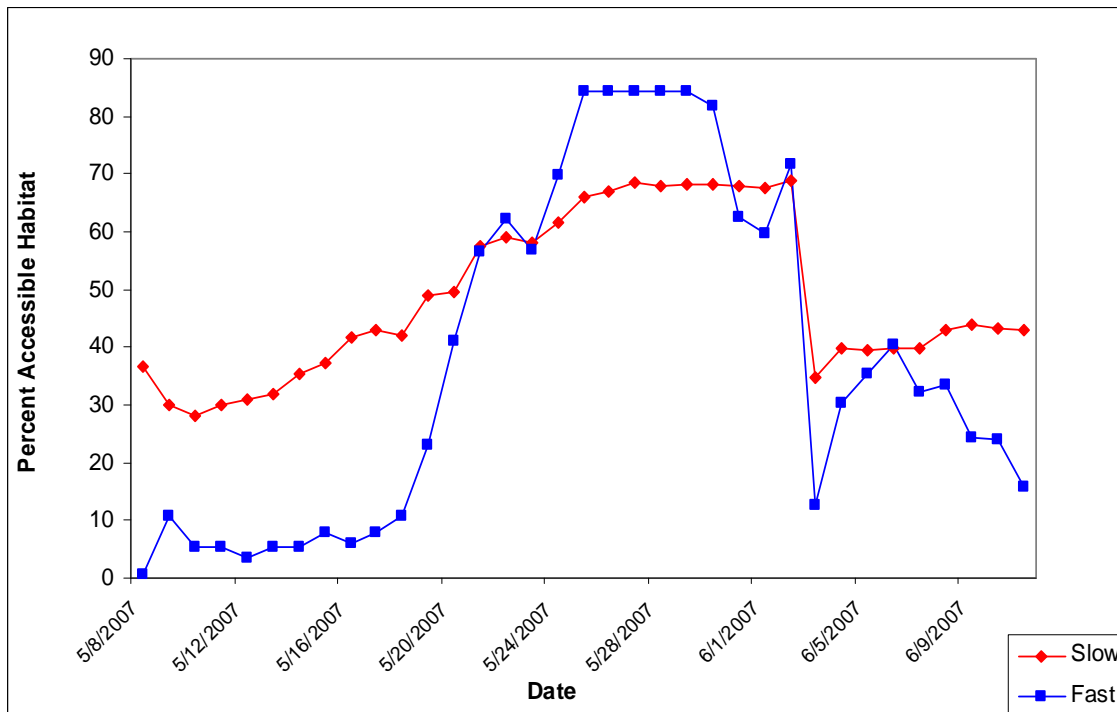
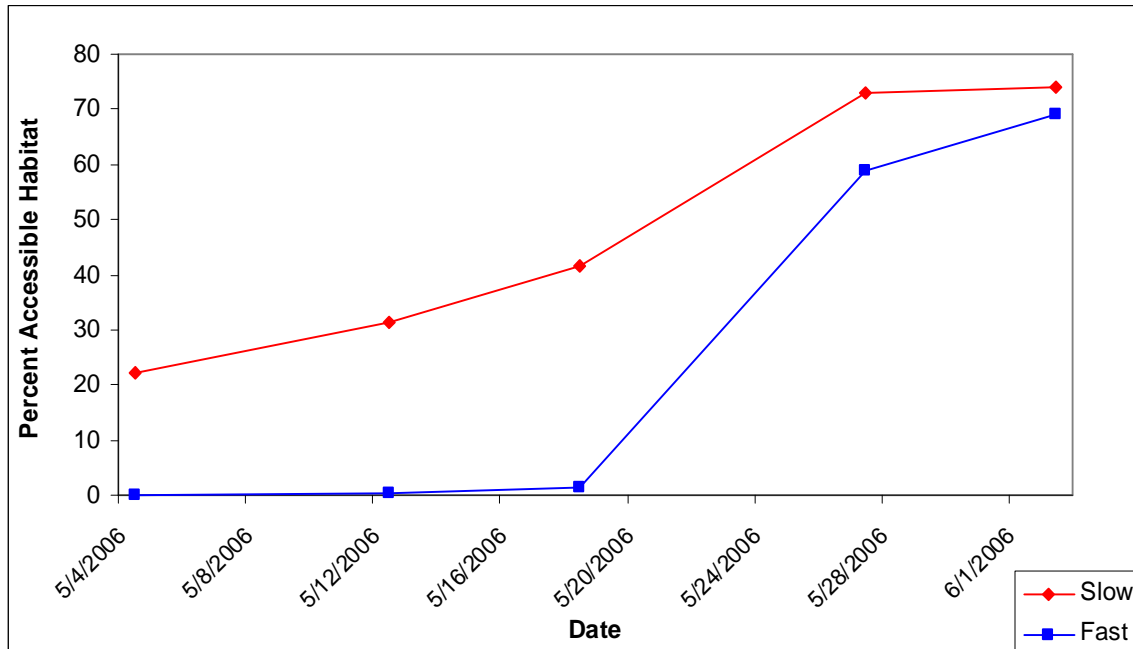


Figure 6. Percent of total area within each managed wetland treatment (slow or fast draw down) made accessible (0-4cm depth) for Semipalmated Sandpipers at the Tom Yawkey Wildlife Center, South Carolina. Top panel (6a) depicts seasonal pattern in 2006; bottom panel (6b) depict pattern in 2007. The fast draw down was implemented on 17 May 2006 and 17 May 2007.

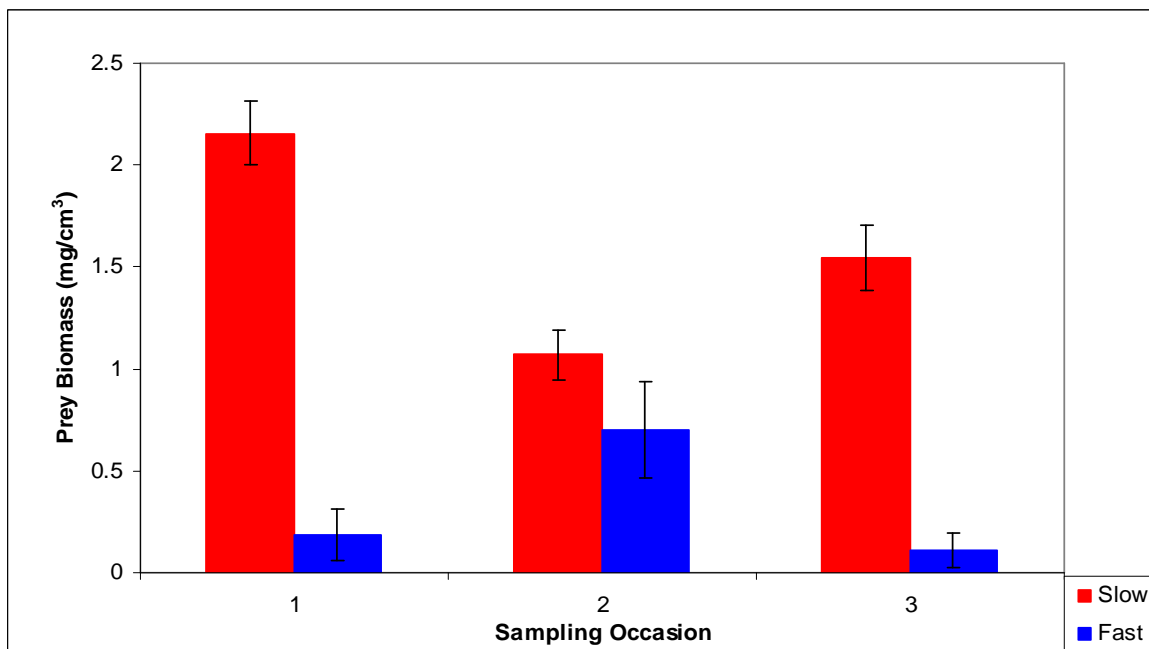
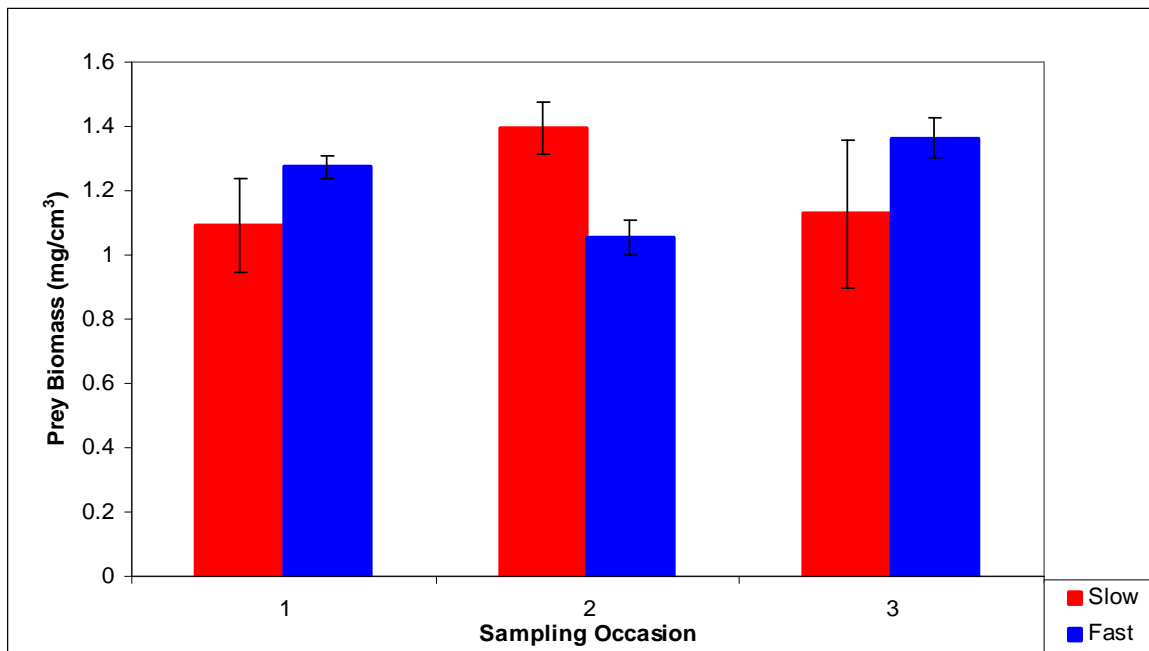


Figure 7. Average biomass (mg/cm^3) of all invertebrates present in muddy substrate and water column in slow- and fast-managed wetland units at the Tom Yawkey Wildlife Center, South Carolina during spring migration of Semipalmated Sandpipers. Top panel (7a) depicts average biomass (\pm SE) of invertebrates sampled on three occasions in 2006: April 28th-30th, May 16th-17th, and June 1st-4th. Bottom panel (7b) depicts average biomass (\pm SE) of invertebrates sampled on May 17th-18th, May 24th-25th, and May 31st-June 1st 2007.

Table 2. Model selection for residency rates (S) at and movement rates (Psi, ψ) between slow- and fast-managed wetland units of Semipalmated Sandpipers at the Tom Yawkey Wildlife Center, South Carolina, Spring 2006. Model parameters include Δ AICc values, AICc weights, number of model parameters, and deviance. Five covariates were used to model residency and movement rates: estimated percent fat (epf), southerly wind speed (Swind), index of bird density (birds/ha), proportion of accessible habitat/treatment (access), and total area under a specific treatment (area). These covariates were modeled as additive effects on either constant or time-varying residency and movement models using reduced parameter models. Time-varying models were also modeled using a linear (T) or quadratic (TT) term. Resight probabilities (p) were modeled as constant (.) and time varying (t). Covariates and interaction between epf and Swind (*) were modeled as additive (+) effects. Only models with a Δ AICc ≤ 10 are listed.

Model	Delta AICc	AICc Weight	#Par	Deviance
{S (TT+epf+Swind+epf*Swind), p (.), Psi (TT+access)}	0	0.22257	11	1241.302
{S (TT+epf+Swind+epf*Swind), p (.), Psi (TT+bird)}	0.59	0.16579	11	1241.891
{S (TT+bird+epf+Swind+epf*Swind), p (.), Psi (TT+access)}	0.92	0.14074	12	1240.139
{S (TT+bird+epf+Swind+epf*Swind), p (.), Psi (TT+bird)}	1.44	0.10809	12	1240.667
{S (TT+access+epf+Swind+epf*Swind), p (.), Psi (TT+access)}	1.97	0.08302	12	1241.195
{S (TT+epf+Swind+epf*Swind), p (.), Psi (TT+access+bird)}	2.06	0.0794	12	1241.284
{S (TT+access+epf+Swind+epf*Swind), p (.), Psi (TT+bird)}	2.54	0.06253	12	1241.762
{S (TT+Swind), p (.), Psi (TT+access)}	3.72	0.0347	9	1249.158
{S (TT+Swind), p (.), Psi (TT+birds)}	4.31	0.02585	9	1249.747
{S (TT+epf+Swind+epf*Swind), p (.), Psi (TT)}	4.48	0.02366	10	1247.858
{S (TT+bird), p (.), Psi (TT+access)}	6.36	0.00928	9	1251.796
{S (TT+access+epf+Swind+epf*Swind), p (.), Psi (TT)}	6.55	0.0084	11	1247.856
{S (TT), p (.), Psi (TT+access)}	6.66	0.00798	8	1254.156
{S (TT+bird), p (.), Psi (TT+bird)}	6.96	0.00685	9	1252.401
{S (TT), p (.), Psi (TT+bird)}	7.25	0.00594	8	1254.745
{S (TT+access), p (.), Psi (TT+access)}	7.44	0.00538	9	1252.884
{S (TT+access), p (.), Psi (TT+bird)}	7.98	0.00411	9	1253.425
{S (TT+Swind), p (.), Psi (TT)}	8.21	0.00366	8	1255.713

Table 3. Beta parameter estimates for the top treatment model of daily survival (\hat{S}), detection (\hat{p}), and movement probabilities ($\hat{\psi}$) of Semipalmated Sandpipers at the Yawkey Wildlife Center, South Carolina, Spring 2006. Covariates were modeled as additive effects on time-varying, reduced parameter models. Additive effects included the interaction between estimated percent fat (epf) and southerly wind speed (Swind).

Model Term	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
<u>Daily Survival</u> (\hat{S})				
Intercept	1.51418	1.27431	-0.98348	4.01184
T (linear)	0.07034	0.11899	-0.16288	0.30355
TT (curvilinear)	-0.00680	0.00587	-0.01831	0.00471
Epf	0.13192	0.05035	0.03323	0.23061
Swind	-0.07357	0.16458	-0.39615	0.24901
Epf*Swind	-0.01774	0.00773	-0.03290	-0.00258
<u>Detection</u> (\hat{p})				
Intercept (constant)	-2.41388	0.14338	-2.69491	-2.13285
<u>Daily Movement</u> ($\hat{\psi}$)				
Intercept	-5.03676	2.49920	-9.93519	-0.13833
T (linear)	1.89467	0.54385	0.82872	2.96061
TT (curvilinear)	-0.11722	0.03134	-0.17865	-0.05580
Access	-2.44691	1.21599	-4.83026	-0.06356

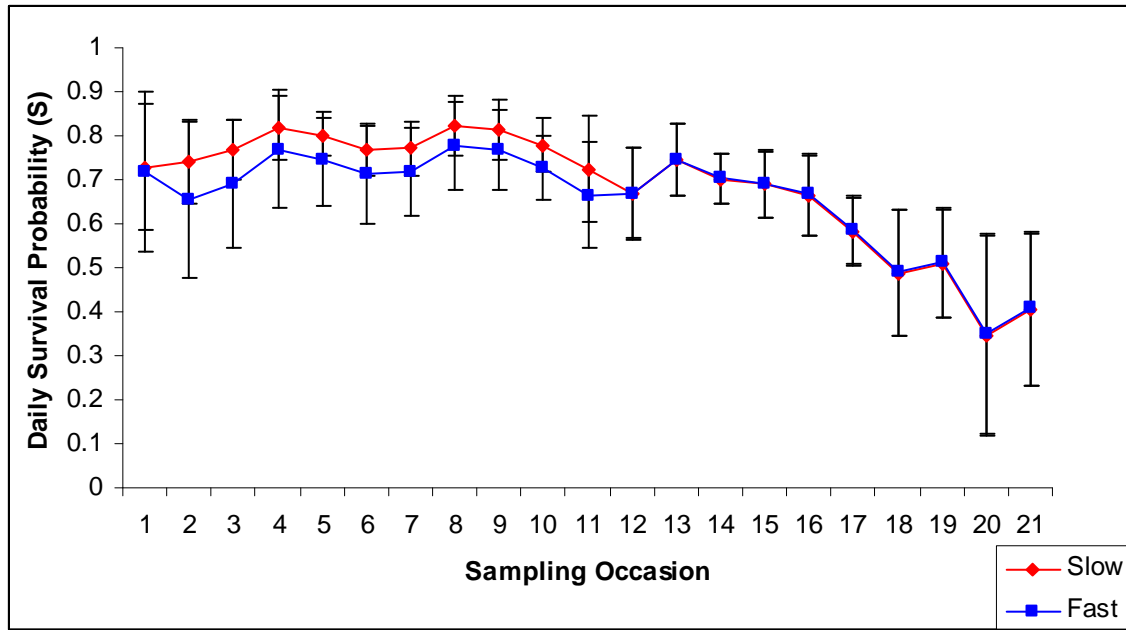


Figure 8. Residency rates (i.e., daily survival probability, \hat{S}) and 95% confidence intervals for Semipalmated Sandpipers in fast- and slow-managed wetland units at the Tom Yawkey Wildlife Center, Spring 2006. Values were obtained after averaging the top five models (i.e., $\Delta AICc \leq 2$, Table 2). The first sampling occasion was May 10th and the last on June 6th. The blue line is the daily residency rate for birds in fast-managed wetland units; the red line for slow-managed units.

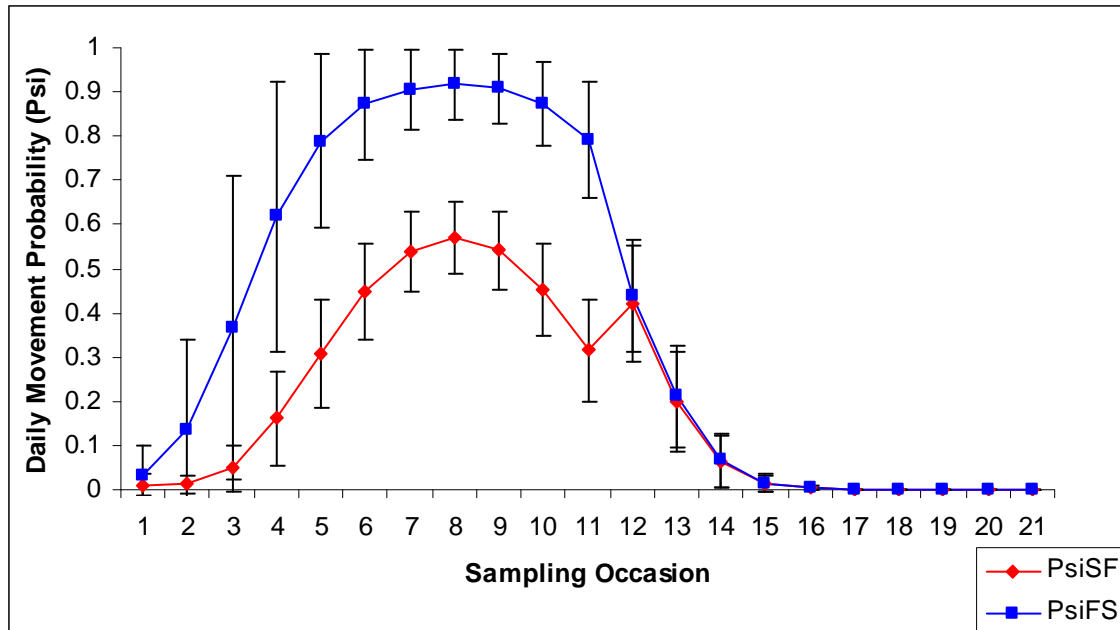


Figure 9. Movement rates (i.e., daily movement probability, $\hat{\psi}$) and 95% confidence intervals for Semipalmated Sandpipers in fast- and slow-managed wetland units at the Tom Yawkey Wildlife Center, Spring 2006. Values were obtained after averaging the top five models (i.e., $\Delta AICc \leq 2$, Table 2). The first sampling occasion was May 10th and the last on June 6th. The blue line is the daily movement rate for birds in fast-managed wetland units; the red line for slow-managed units.

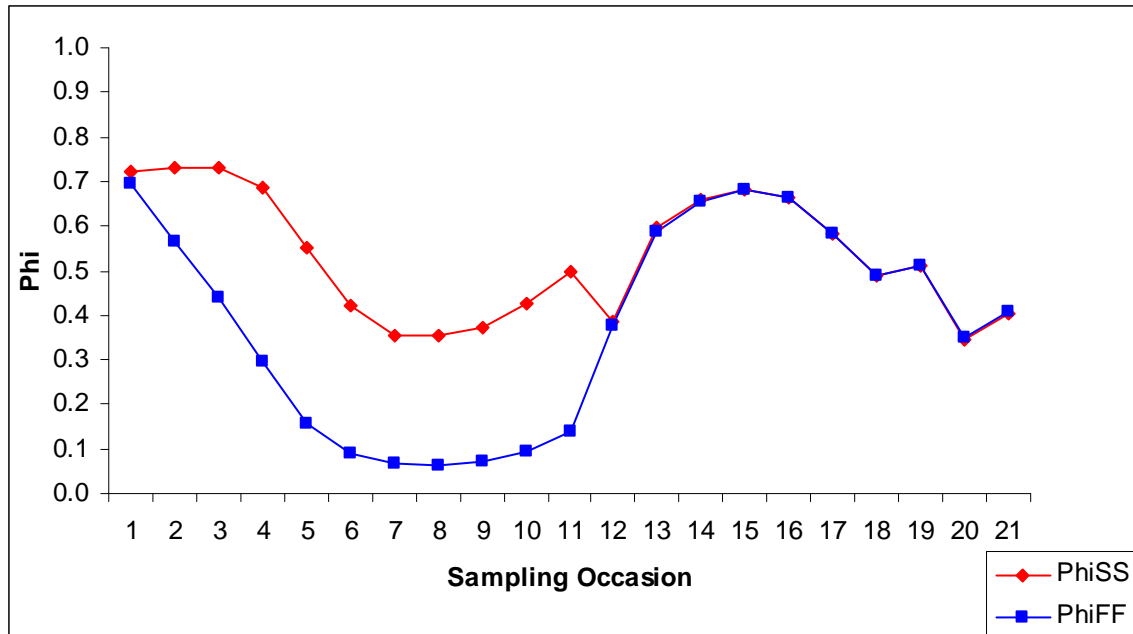


Figure 10. Seasonal patterns of the probability of surviving and staying at slow-managed wetland units (Phi SS, $\hat{\Phi}^{SS}$) and of surviving and staying in fast-managed units (Phi FF, $\hat{\Phi}^{FF}$) by Semipalmated Sandpipers at the Yawkey Wildlife Center, South Carolina during Spring 2006. Values were obtained after averaging the top five models (i.e., $\Delta AICc \leq 2$, Table 2). The first sampling occasion was May 10th and the last on June 6th.

Table 4. Model selection for residency rates (S) at and movement rates (Psi, ψ) between slow- and fast-managed wetland units of Semipalmated Sandpipers at the Tom Yawkey Wildlife Center, South Carolina, Spring 2007. Model parameters include Δ AICc values, AICc weights, number of model parameters, and deviance. Seven covariates were used to model residency and movement rates: estimated percent fat (epf), southerly wind speed (Swind), index of bird density (birds/ha), prey biomass (mg/cm³), proportion of accessible habitat/treatment (access), average distance between treatments (proximity), and total area under a specific treatment (area). These covariates were modeled as additive effects on either constant or time-varying residency and movement models using reduced parameter models. Models included interaction terms (*) for epf and Swind, prey and access, and linear (T) or quadratic (TT) terms. Encounter probabilities (p) were modeled as constant (.), time varying (t), and by encounter source (i.e., resight, telemetry). Only models with a Δ AICc \leq 10 are listed.

Model	Delta AICc	AICc Weight	#Par	Deviance
{S (TT+bird+epf+Swind+epf*Swind), p (gTRT), Psi (TRT+TT+prey)}	0	0.24024	14	2232.752
{S (TT+prey+epf+Swind+epf*Swind+bird), p (gTRT), Psi (TRT+TT+prey)}	1.57	0.10957	15	2232.254
{S (TT+access+epf+Swind+epf*Swind+bird), p (gTRT), Psi (TRT+TT+prey)}	1.82	0.09689	15	2232.5
{S (TT+prey+epf+Swind+epf*Swind+bird), p (gTRT), Psi (TRT+TT+prey+bird)}	1.96	0.09004	15	2232.647
{S (TT+prey+epf+Swind+epf*Swind), p (gTRT), Psi (TRT+TT+prey)}	2.34	0.07441	14	2235.096
{S (TT+prey+epf+Swind+epf*Swind+bird), p (gTRT), Psi (TRT+TT+bird)}	2.69	0.06258	15	2233.375
{S (TT+prey+epf+Swind+epf*Swind), p (gTRT), Psi (TRT+TT+bird)}	3.39	0.04417	14	2236.139
{S (TT+prey+access+prey*access+epf+Swind+epf*Swind), p (gTRT), Psi (TRT+TT+prey)}	3.92	0.03383	16	2232.532
{S (TT+epf+Swind+epf*Swind), p (gTRT), Psi (TRT+TT+prey)}	3.98	0.03288	13	2238.792
{S (TT+prey+epf+Swind+epf*Swind), p (gTRT), Psi (TRT+TT+prey+bird)}	4.14	0.03036	15	2234.821
{S (TT+access+epf+Swind+epf*Swind), p (gTRT), Psi (TRT+TT+prey)}	4.28	0.02825	14	2237.033
{S (TT+prey+access+prey*access+epf+Swind+epf*Swind), p (gTRT), Psi (TRT+TT+bird)}	4.73	0.02261	16	2233.338
{S (TT+prey+epf+Swind+epf*Swind), p (gTRT), Psi (TRT+TT+access)}	4.95	0.02018	14	2237.705
{S (TT+epf+Swind+epf*Swind), p (gTRT), Psi (TRT+TT+bird)}	5.23	0.01757	13	2240.046
{S (TT+epf+Swind+epf*Swind+prey+bird), p (gTRT), Psi (TT+prey+access)}	5.37	0.01636	15	2236.057
{S (TT+access+epf+Swind+epf*Swind), p (gTRT), Psi (TRT+TT+bird)}	5.44	0.01585	14	2238.188
{S (TT+prey+access+prey*access+epf+Swind+epf*Swind), p (gTRT), Psi (TRT+TT+access)}	5.85	0.0129	16	2234.46
{S (TT+prey+epf+Swind+epf*Swind), p (gTRT), Psi (TT+Bird+access)}	6.18	0.01091	14	2238.936
{S (TT+epf+Swind+epf*Swind+prey), p (gTRT), Psi (TT+prey+access)}	6.2	0.01084	14	2238.949
{S (TT+epf+Swind+epf*Swind), p (gTRT), Psi (TRT+TT+access)}	6.51	0.00928	13	2241.323
{S (TT+access+epf+Swind+epf*Swind), p (gTRT), Psi (TRT+TT+access)}	6.99	0.00731	14	2239.738
{S (TT+prey+access+prey*access), p (gTRT), Psi (TRT+TT+Bird)}	9.75	0.00184	13	2244.564

Table 5. Beta parameter estimates for the top treatment model of daily survival (\hat{S}), detection (\hat{p}), and movement probabilities ($\hat{\psi}$) of Semipalmated Sandpipers at the Yawkey Wildlife Center, South Carolina, Spring 2007. Covariates were modeled as additive effects on time-varying, reduced parameter models. Additive effects included the interaction between estimated percent fat (epf) and southerly wind speed (Swind).

Model Term	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
<u>Daily Survival</u> (\hat{S})				
Intercept	-1.44554	1.17131	-3.74131	0.85024
T (linear)	0.18496	0.15301	-0.11493	0.48485
TT (curvilinear)	-0.01023	0.00554	0.02108	0.00063
Ep _f	0.05966	0.01914	0.02215	0.09717
Bird	0.67797	0.30495	0.08027	1.27568
Swind	0.33747	0.09271	0.15575	0.51918
Ep _f *Swind	-0.01084	0.00423	-0.01913	-0.00255
<u>Detection</u> (\hat{p})				
Intercept (telemetry)	0.84881	0.13670	0.58088	1.11675
Resight	-2.91444	0.17947	-3.26620	-2.56267
<u>Daily Movement</u> ($\hat{\psi}$)				
Intercept (Fast)	1.19812	5.01567	-8.63258	11.02882
Slow	-7.22126	3.21949	-13.53146	-0.91107
T (linear)	0.59796	0.42648	-0.23794	1.43386
TT (curvilinear)	-0.02036	0.01594	-0.05162	0.01089
Prey	-1.88630	1.31525	-4.46419	0.69159

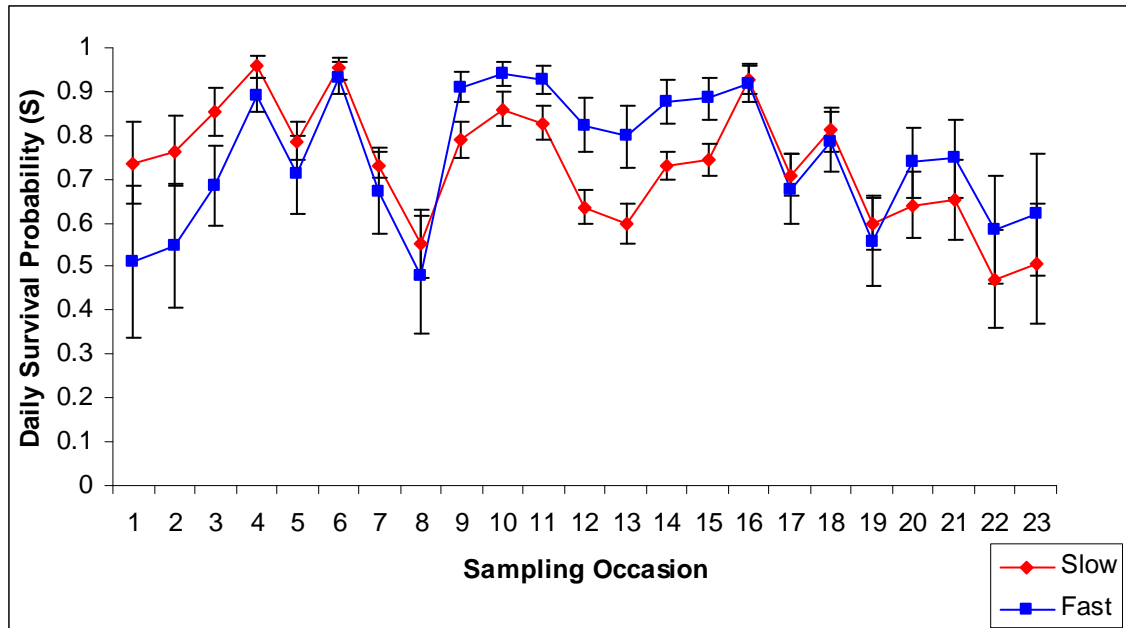


Figure 11. Residency rates (i.e., daily survival probability, \hat{S}) and 95% confidence intervals for Semipalmated Sandpipers in fast- and slow-managed wetland units at the Tom Yawkey Wildlife Center, Spring 2007. Values were obtained after averaging the top four models (i.e., $\Delta AICc \leq 2$, Table 3). The first sampling occasion was May 8th and the last on June 11th. The blue line is the daily residency rate for birds in fast-managed wetland units; the red line for slow-managed units.

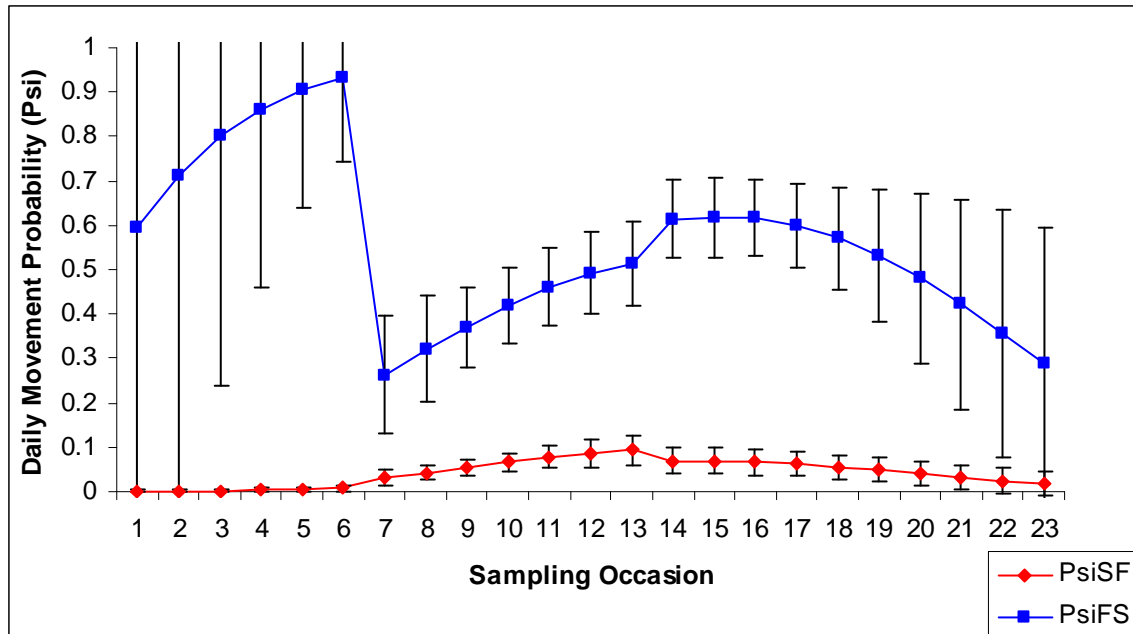


Figure 12. Movement rates (i.e., daily movement probability, $\hat{\psi}$) and 95% confidence intervals for Semipalmated Sandpipers in fast- and slow-managed wetland units at the Tom Yawkey Wildlife Center, Spring 2007. Values were obtained after averaging the top four models (i.e., $\Delta\text{AICc} \leq 2$, Table 3). The first sampling occasion was May 8th and the last on June 11th. The blue line is the daily movement rate for birds in fast-managed wetland units; the red line for slow-managed units. Habitat in fast-managed wetland units was inaccessible (i.e., flooded) during the first six sampling occasions.

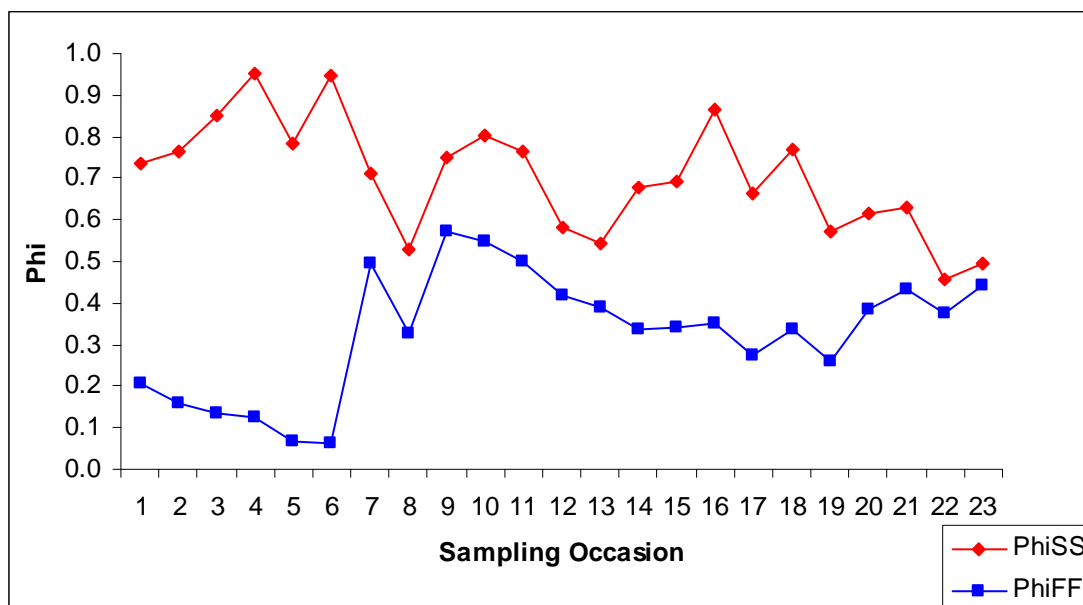


Figure 13. Seasonal patterns of the probability of surviving and staying at slow-managed wetland units (Φ_{SS} , $\hat{\Phi}^{SS}$) and of surviving and staying at fast-managed units (Φ_{FF} , $\hat{\Phi}^{FF}$) by Semipalmated Sandpipers at the Yawkey Wildlife Center, South Carolina during Spring 2007. Values were calculated based on daily survival (\hat{S}) and movement ($\hat{\psi}$) probabilities obtained after averaging the top four models (i.e., $\Delta AICc \leq 2$, Table 3). The first sampling occasion was May 8th and the last on June 11th.

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Appendices

Appendix I. List of invertebrate taxa detected (present/absent) in either slow- or fast-managed wetland units at The Tom Yawkey Wildlife Center, South Carolina, Spring 2006 and 2007. Summary includes average prey biomass (mg/cm³) by sampled substrate (e.g., mud, water column) by sampled substrate (mud or water column) and combined (all taxa, all substrates). Average prey biomass by substrate or combined and treatment (slow or fast) were compared using ANOVA. Statistical differences ($p < 0.05$) between any pair of treatment are indicated by an asterisk. Presence in the sample is denoted by 1; absence by 0.

2006 Invertebrate Sampling Summary

	Presence/Absence		Mud Density		Water Density		Combined Mud and Water Density	
	Fast	Slow	Slow	Fast	Slow	Fast	Slow	Fast
Polychaeta	1	1	0.011925	0.027008	0.000991	0.000139	0.012916	0.027147
Chironomidae	1	1	0.001164	0.006298	0.000230	0.000290	0.001394	0.006588
Oligochaeta	1	0	0	0	0	0.000001	0	0.000001
Diptera	1	1	0.000168	0.000548	0	0	0.000168	0.000548
Amphipoda	1	1	0.000281	0.001879	0.002559	0.000043	0.002841	0.001922
Odonata	0	1	0	0	0.000021	0	0.000021	0
Gastropod	1	1	0.010092	0.000225	0.000419	0.000016	0.010511	0.000241
Corixidae	1	1	0.000238	0	0.003236	0.000396	0.003473	0.000396
Coleoptera	0	0	0	0	0	0	0	0
Trichoptera	1	0	0	0	0	0.000252	0	0.000252

2007 Invertebrate Sampling Summary

	Presence/Absence		Mud Density		Water Density		Combined Mud and Water Density	
	Fast	Slow	Slow	Fast	Slow	Fast	Slow	Fast
Polychaeta	1	1	0.076194	0.011940	0.000786	0.002440	0.076980	0.014381
Chironomidae	1	1	0.008244	0.017190	0.001514	0.004993	0.009759	0.022184
Oligochaeta	1	1	0.002660	0.000029	0.000017	0.000040	0.002677	0.000069
Diptera	1	1	0.000022	0.000209	0.000027	0.000084	0.000049	0.000294
Amphipoda	1	1	0.143879	0.000173	0.000913	0.008930	0.144792	0.009103
Odonata	1	1	0.000000	0.000154	0.000009	0.000923	0.000009	0.001077*
Gastropod	1	1	0.011702	0.071278	0.004479	0.071826	0.016180	0.143105*
Corixidae	1	1	0.000544	0.001532	0.000615	0.006173	0.001159	0.007705*
Coleoptera	1	0	0	0.000118	0	0	0	0.000118
Trichoptera	0	1	0.000367	0	0	0	0.000367	0

Appendix II. List of *a priori* models used to assess daily residency (\hat{S}) and movement ($\hat{\psi}$) rates between slow- and fast-managed wetland units of Semipalmated Sandpipers at the Tom Yawkey Wildlife Center, South Carolina, Spring 2006.

Naïve, Area and Proximity Models - Constant S and Psi, Constant p

$$\begin{aligned} S^{(.)} p^{(.)} \psi^{(.)} \\ S^{(t)} p^{(.)} \psi^{(t)} \\ S^{(t)} p^{(t)} \psi^{(t)} \\ S^{(.)} p^{(.)} \psi^{TRT} \\ S^{TRT} p^{(.)} \psi^{(.)} \\ S^{(.)} p^{(TRT)} \psi^{(.)} \\ S^{TRT} p^{(.)} \psi^{TRT} \\ S^{Area} p^{(.)} \psi^{TRT} \\ S^{TRT} p^{(.)} \psi^{Area} \\ S^{(.)} p^{(.)} \psi^{Area} \\ S^{epf} p^{(.)} \psi^{TRT} \end{aligned}$$

$$\begin{aligned} S^{TT+access} p^{(.)} \psi^{TT} \\ S^{TT+birds} p^{(.)} \psi^{TT} \\ S^{TT+Swind} p^{(.)} \psi^{TT} \\ S^{TT+access} p^{(.)} \psi^{TT+access} \\ S^{TT+access} p^{(.)} \psi^{TT+birds} \\ S^{TT+birds} p^{(.)} \psi^{TT+access} \\ S^{TT+birds} p^{(.)} \psi^{TT+birds} \\ S^{TT+Swind} p^{(.)} \psi^{TT+access} \\ S^{TT+Swind} p^{(.)} \psi^{TT+birds} \end{aligned}$$

Time-varying Models (epf, access, Swind, birds)

$$\begin{aligned} S^T p^{(.)} \psi^T \\ S^{TT} p^{(.)} \psi^{TT} \\ S^{TT} p^{(.)} \psi^{TT+access} \\ S^{TT} p^{(.)} \psi^{TT+birds} \end{aligned}$$

$$\begin{aligned} S^{TT+epf+Swind+epf*Swind} p^{(.)} \psi^{TT} \\ S^{TT+epf+Swind+epf*Swind} p^{(.)} \psi^{TT+access} \\ S^{TT+epf+Swind+epf*Swind} p^{(.)} \psi^{TT+birds} \\ S^{TT+epf+Swind+epf*Swind} p^{(.)} \psi^{TT+access+birds} \\ S^{TT+access+epf+Swind+epf*Swind} p^{(.)} \psi^{TT} \\ S^{TT+access+epf+Swind+epf*Swind} p^{(.)} \psi^{TT+access} \\ S^{TT+access+epf+Swind+epf*Swind} p^{(.)} \psi^{TT+birds} \\ S^{TT+birds+epf+Swind+epf*Swind} p^{(.)} \psi^{TT+access} \\ S^{TT+birds+epf+Swind+epf*Swind} p^{(.)} \psi^{TT+birds} \end{aligned}$$

Appendix III. List of *a priori* models used to assess daily residency (\hat{S}) and movement ($\hat{\psi}$) rates between slow- and fast-managed wetland units of Semipalmated Sandpipers at the Tom Yawkey Wildlife Center, South Carolina, Spring 2007.

Naïve, Area and Proximity Models - Constant S Psi, p by group (i.e., Resight and Telemetry)

$$\begin{aligned} S^{(.)} p^{(.)} \psi^{(.)} \\ S^{(t)} p^{(g)} \psi^{(.)} \\ S^{(t)} p^{(g)} \psi^{(t)} \\ S^{TRT} p^{(g)} \psi^{(.)} \\ S^{(.)} p^{(g)} \psi^{TRT} \\ S^{TRT} p^{(g)} \psi^{TRT} \\ S^{area} p^{(g)} \psi^{TRT} \\ S^{area} p^{(g)} \psi^{proximity} \\ S^{TRT} p^{(g)} \psi^{proximity} \end{aligned}$$

Time-varying Models, p by group (epf, prey, access, Swind, area, proximity)

$$\begin{aligned} S^{TT} p^{(g)} \psi^{proximity} \\ S^{TT+access} p^{(g)} \psi^{area} \\ S^{TT+access} p^{(g)} \psi^{proximity} \\ S^{TT+birds} p^{(g)} \psi^{proximity} \\ S^{TT+prey} p^{(g)} \psi^{area} \\ S^{TT+prey} p^{(g)} \psi^{proximity} \\ S^{TT+Swind} p^{(g)} \psi^{proximity} \\ \\ S^{TT+epf+Swind+epf*Swind} p^{(TRT(g))} \psi^{area} \\ S^{TT+epf+Swind+epf*Swind} p^{(TRT(g))} \psi^{proximity} \\ S^{TT+prey+access+prey*access} p^{(TRT(g))} \psi^{area} \\ S^{TT+prey+access+prey*access} p^{(TRT(g))} \psi^{proximity} \end{aligned}$$

$$\begin{aligned} S^{TRT+T} p^{(TRT(g))} \psi^{TRT+T} \\ S^{TRT+TT} p^{(TRT(g))} \psi^{TRT+TT} \end{aligned}$$

$$\begin{aligned} S^{TT+access} p^{(TRT(g))} \psi^{TRT+TT+access} \\ S^{TT+access} p^{(TRT(g))} \psi^{TRT+TT+birds} \\ S^{TT+access} p^{(TRT(g))} \psi^{TRT+TT+prey} \\ S^{TT+birds} p^{(TRT(g))} \psi^{TRT+TT+access} \\ S^{TT+birds} p^{(TRT(g))} \psi^{TRT+TT+birds} \\ S^{TT+birds} p^{(TRT(g))} \psi^{TRT+TT+prey} \\ S^{TT+prey} p^{(TRT(g))} \psi^{TT+prey} \\ S^{TT+prey} p^{(TRT(g))} \psi^{TRT+TT+access} \\ S^{TT+prey} p^{(TRT(g))} \psi^{TRT+TT+birds} \end{aligned}$$

$$\begin{aligned}
S^{TT+Swind} p^{(TRT(g))} \Psi^{TRT+TT+access} \\
S^{TT+Swind} p^{(TRT(g))} \Psi^{TRT+TT+birds} \\
S^{TT+Swind} p^{(TRT(g))} \Psi^{TRT+TT+prey}
\end{aligned}$$

$$\begin{aligned}
S^{TT+birds+epf+Swind+epf*Swind} p^{(TRT(g))} \Psi^{TT+prey} \\
S^{TT+prey+epf+Swind+epf*Swind} p^{(TRT(g))} \Psi^{TT+prey+access} \\
S^{TT+prey+epf+Swind+epf*Swind} p^{(TRT(g))} \Psi^{TT+birds+access} \\
S^{TT+prey+birds+epf+Swind+epf*Swind} p^{(TRT(g))} \Psi^{TT+birds} \\
S^{TT+prey+birds+epf+Swind+epf*Swind} p^{(TRT(g))} \Psi^{TT+prey} \\
S^{TT+prey+birds+epf+Swind+epf*Swind} p^{(TRT(g))} \Psi^{TT+prey+access} \\
S^{TT+prey+birds+epf+Swind+epf*Swind} p^{(TRT(g))} \Psi^{TT+birds+prey}
\end{aligned}$$

$$\begin{aligned}
S^{TT+epf+Swind+epf*Swind} p^{(TRT(g))} \Psi^{TRT+TT+access} \\
S^{TT+epf+Swind+epf*Swind} p^{(TRT(g))} \Psi^{TRT+TT+birds} \\
S^{TT+epf+Swind+epf*Swind} p^{(TRT(g))} \Psi^{TRT+TT+prey} \\
S^{TT+prey+access+prey*access} p^{(TRT(g))} \Psi^{TRT+TT+access} \\
S^{TT+prey+access+prey*access} p^{(TRT(g))} \Psi^{TRT+TT+birds} \\
S^{TT+birds+prey+access+prey*access} p^{(TRT(g))} \Psi^{TRT+TT+birds} \\
S^{TT+prey+epf+Swind+epf*Swind} p^{(TRT(g))} \Psi^{TRT+TT+access} \\
S^{TT+prey+epf+Swind+epf*Swind} p^{(TRT(g))} \Psi^{TRT+TT+birds} \\
S^{TT+prey+epf+Swind+epf*Swind} p^{(TRT(g))} \Psi^{TRT+TT+prey} \\
S^{TT+prey+epf+Swind+epf*Swind} p^{(TRT(g))} \Psi^{TRT+TT+prey+birds} \\
S^{TT+access+epf+Swind+epf*Swind} p^{(TRT(g))} \Psi^{TRT+TT+access} \\
S^{TT+access+epf+Swind+epf*Swind} p^{(TRT(g))} \Psi^{TRT+TT+birds} \\
S^{TT+access+epf+Swind+epf*Swind} p^{(TRT(g))} \Psi^{TRT+TT+prey} \\
S^{TT+access+birds+epf+Swind+epf*Swind} p^{(TRT(g))} \Psi^{TRT+TT+prey}
\end{aligned}$$

$$\begin{aligned}
S^{TT+ epf+Swind+epf*Swind+prey+access+prey*access} p^{(TRT(g))} \Psi^{TRT+TT+access} \\
S^{TT+ epf+Swind+epf*Swind +prey+access+prey*access} p^{(TRT(g))} \Psi^{TRT+TT+birds} \\
S^{TT+ epf+Swind+epf*Swind+prey+access+prey*access} p^{(TRT(g))} \Psi^{TRT+TT+prey}
\end{aligned}$$